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Galeus gracilis n.sp., a New Sawtail Catshark from Australia, with Comments on the Systematics of the Genus *Galeus* Rafinesque, 1810 (Carcharhiniformes: Scyliorhinidae)

L.J.V. COMPAGNO[1] & J.D. STEVENS[2]

[1] Shark Research Centre, South African Museum,
PO Box 61, Cape Town 8000, South Africa

[2] CSIRO Division of Fisheries, Marine Laboratories,
GPO Box 1538, Hobart, Tas. 7001, Australia

ABSTRACT. *Galeus gracilis* n.sp. (Scyliorhinidae: Pentanchinae: Galeini) is described from the uppermost slope of Western Australia and the Northern Territory. It is the second recognised member of its genus from Australian waters. This small, slender-bodied *Galeus* is distinguished from the 12 other species in the genus by a combination of proportional dimensions, tooth-row counts, clasper morphology, pectoral-fin radial counts, vertebral counts, intestinal valve counts, chondrocranial morphology, and colouration. It is closest to three Japanese species: *G. eastmani*, *G. longirostris* and *G. nipponensis*. *Galeus gracilis* is compared in detail to *G. boardmani* from southern Australia, which differs from it in numerous features.

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The sawtail catsharks, genus *Galeus* Rafinesque, 1810 (Scyliorhinidae: Pentanchinae: Galeini), were most recently reviewed by Compagno (1988), who recognised 11 species following the work of Cadenat (1959), Springer (1966, 1979), Springer & Wagner (1966), Nakaya (1975), Cadenat & Blache (1981), Compagno (1984), and Muñoz-Chapuli & Ortega (1985). While Compagno's review was in press, Tachikawa & Taniuchi (1987) described a 12th valid species from Japan.

The geographic distribution of *Galeus* species is spotty and disjunct. The known species cluster by region and show considerable sympatry in the eastern Atlantic and western North Pacific (Compagno, 1988):

Western North Atlantic: *Galeus arae* (Nichols, 1927), South Carolina south to Caribbean and Colombia.

Eastern Atlantic: *Galeus melastomus* Rafinesque, 1810, Faroes and Norway south to Mediterranean and Senegal; *G. murinus* (Collett, 1904), Iceland and Faroes; *G. atlanticus* (Vaillant, 1888), Morocco and Spain; *G. polli* Cadenat, 1959, southern Morocco to central Namibia.

Australia: *Galeus boardmani* (Whitley, 1928), south coast from Western Australia to New South Wales.

Western North Pacific: *Galeus eastmani* (Jordan & Snyder, 1904), Japan, possibly Vietnam and the East

China Sea; *G. sauteri* (Jordan & Richardson, 1909), Taiwan, possibly Japan and Philippines; *G. schultzi* Springer, 1979, Philippines; *G. nipponensis* Nakaya, 1975 and *G. longirostris* Tachikawa & Taniuchi, 1987, Japan.

Eastern Pacific: *Galeus piperatus* Springer & Wagner, 1966, northern Gulf of California.

Recent offshore trawl surveys on the outer continental shelves and upper slopes of Australia (Gloerfelt-Tarp & Kailola, 1984; Davis & Ward, 1984; Sainsbury *et al.*, 1985; Gorman & Graham, 1985; Williams, 1987) has produced a wealth of scyliorhinid catsharks along with many other sharks and bony fishes. Compagno (1984, 1988) noted the presence of an undescribed species of *Galeus* off Western Australia that is very different from the Australian species *G. boardmani* but is closer to the western North Pacific *G. eastmani*, *G. nipponensis* and *G. longirostris*. It differs from these species in vertebral counts, e xternal and cranial morphology, morphometrics and colouration; we describe it below as *Galeus gracilis* n.sp.

The purpose of this paper is to describe this new species and to compare it with the other known species of the genus.

Terminology and Abbreviations

The terminology for external structures, chondrocrania, vertebrae and dentition follows Compagno (1970, 1988). For vertebrae, an additional abbreviation PC is introduced for precaudal (monospondylous + diplospondylous precaudal) vertebral counts. The abbreviations and methods of measuring follow the FAO system of Compagno (1984), except that the measurement MOL (mouth length) was incorrectly shown in the diagram (Compagno, 1984: 12) as extending from the lower symphysis to the mouth corners; it should be from the *upper* symphysis to the mouth corners. Also, TL is used for total length and PCL for precaudal length (following general usage in ichthyology) instead of TOT and PRC. The abbreviations for measurements in this account include: TL (TOT) – total length; PCL (PRC) – precaudal length; PRN – prenarial length; POR – preoral length; POB – preorbital length; PSP – prespiracle length; PGI – pregill (prebranchial) length; HDL – head length; PP1 – prepectoral length; PP2 – prepelvic length; SVL – snout-vent length; PAL – preanal length; PD1 – pre-first dorsal length; PD2 – pre-second dorsal length; IDS – interdorsal space; DCS – dorsocaudal space; PPS – pectoral-pelvic space; PAS – preanal space; ACS – anal-caudal space; EYL – eye length; EYH – eye height; INO – interorbital width; NOW – nostril width; INW – internarial width; ANF – anterior nasal flap length; SPL – spiracle length; ESL – eye-spiracle length; MOL – mouth length; MOW – mouth width; ULA – upper labial furrow length; LLA – lower labial furrow length; GS1 – first gill opening height; GS2 – second gill opening height; GS3 – third gill opening height; GS4 – fourth gill opening height; GS5 – fifth gill opening height; HDH – head height; HDW – head width; TRH – trunk height; TRW – trunk width; CPH – caudal peduncle height; CPW – caudal peduncle width; GIR – girth; P1L – pectoral length; P1A – pectoral anterior margin; P1B – pectoral base; P1H – pectoral height; P1I – pectoral inner margin; P1P – pectoral posterior margin; P2L – pelvic length; P2A – pelvic anterior margin; P2B – pelvic base; P2H – pelvic height; P2I – pelvic inner margin; P2P – pelvic posterior margin; CLO – clasper outer length; CLI – clasper inner length; CLB – clasper base width; D1L – first dorsal length; D1A – first dorsal anterior margin; D1B – first dorsal base; D1H – first dorsal height; D1I – first dorsal inner margin; D1P – first dorsal posterior margin; D2L – second dorsal length; D2A – second dorsal anterior margin; D2B – second dorsal base; D2H – second dorsal height; D2I – second dorsal inner margin; D2P – second dorsal posterior margin; ANL – anal length; ANA – anal anterior margin; ANB – anal base; ANH – anal height; ANI – anal inner margin; ANP – anal posterior margin; CDM – dorsal caudal margin; CPV – preventral caudal margin; CPL+U – combined lower and upper postventral caudal margin; CST – subterminal caudal margin; CTR – terminal caudal margin; CTL – terminal caudal lobe; DAO – second dorsal-anal origin; DAI – second dorsal-anal insertion. NBL is for nasobasal length, the distance from the base of the medial rostral cartilage to the occipital centrum of the chondrocranium. Pectoral radial counts include all radials and combine free mesopterygial and metapterygial radials with the fused proximal segments of the propterygial and first two mesopterygial radials, which are counted as three additional radials (Fig.5). This is unlike the method of Muñoz-Chapuli & Ortega (1985), who counted only the free radials.

Abbreviations and prefixes for field, accession, and catalogue numbers follow Leviton *et al.* (1986) and Compagno (1988), or have been coined specially: Annnn, 0nn, nnnn or Enn – RV *Africana* station, cruise, and block or experimental station number, Sea Fisheries Research Institute, Cape Town; AMS – Australian Museum, Sydney; CAS – California Academy of Sciences, San Francisco; CSIRO CA and CSIRO H – CSIRO Marine Laboratories, Hobart, Tasmania; DAE – D.A. Ebert field number; ISH – Institut fur Seefischerei, Hamburg; LJVC – L.J.V. Compagno catalogued collection; ORE – RV *Oregon* station number, US National Marine Fisheries Service; QM – Queensland Museum, Brisbane; RUSI – J.L.B. Smith Institute of Ichthyology, Grahamstown; SO – CSIRO RV *Soela* station number; SAM – South African Museum, Cape Town; SB – RV *Silver Bay* station number, US National Marine Fisheries Service; SU – Stanford University Division of Systematic Biology fish collection – now housed at CAS; WAM, Western Australian Museum, Perth. Abbreviations for statistics: cv – coefficient of variation (100 x standard deviation/mean); n – number of specimens; sd – standard deviation.

All tables are listed in the Appendix.

Schyiorhinidae Gill, 1862

Pentanchinae Smith & Radcliffe, 1912

Galeini Fowler, 1934

Comments. Compagno (1988) presented discussions and definitions of the subfamilies and tribes of Scyliorhinidae. The Pentanchinae includes the tribes Pentanchini and Galeini, of which the Galeini is the most diverse in genera.

Galeus Rafinesque, 1810

Galeus Rafinesque, 1810: 13. Type species *Galeus melastomus* Rafinesque, 1810, by subsequent designation of Fowler, 1908: 53.

Definition. Slender-bodied to moderately stout, cylindrical to compressed, long-headed catsharks with firm skin and well-calcified dermal denticles. Stomach not inflatable. Tail moderately long, length from vent to lower caudal origin about 0.4-0.8 of snout-vent length. Snout moderately long, rounded-parabolic or angular in dorsoventral view, usually pointed in lateral view; snout without greatly enlarged ampullal pores. Nostrils enlarged but with incurrent and excurrent apertures only partly open to exterior; anterior nasal flaps small, low, angular, well separated from the midline and ending in front of mouth. No nasoral grooves. Eyes dorsolateral or nearly lateral on head, with subocular grooves narrow to non-existent. Mouth angular or semiangular, teeth prominently exposed in ventral view of head. Labial furrows on both jaws moderately long, uppers ending well behind lower symphysis. Branchial region short, gill slits lateral on head. Posterior teeth not differentiated at distal ends of dental bands. Two dorsal fins present, about equal-sized; origin of first dorsal varying from over pelvic-fin midbases to over their insertions; second dorsal-fin origin over the last half of the anal-fin base. Inner margins of pelvic fins not fused over claspers in adult males of most species (*G. boardmani*, an exception). Claspers without an anterior tab on cover rhipidion; pseudosiphon short; clasper tip without a papillose brush. Anal fin large and more or less elongated, larger than dorsal fins and variably smaller or larger than pelvic fins; anal origin varying from close to pelvic-fin insertions to far behind pelvic bases, and insertion varying from well anterior to adjacent to lower caudal-fin origin. Caudal fin more or less elongated, over a fifth of total length in adults, with crests of enlarged denticles on the dorsal and sometimes preventral caudal margins. Supraorbital crests absent from cranium. Vertebral centra weakly calcified, with intermedialia hardly developed and without diagonal calcifications. Total vertebral counts 115-150. Colour pattern of dark saddles and blotches variably present or absent, no small dark or light spots.

For comprehensive definitions, synonymies and discussions of the nomenclature, systematics, and relationships of this genus see Springer (1979) and Compagno (1984, 1988).

Comparative Material

Galeus arae. All from western North Atlantic: FLORIDA STRAITS: SB 2420, 305 mm TL adult male, 24°14'S 81°24'W, South of Key West. GULF OF MEXICO, off Mississippi Delta: SB 3515, 2 females, 275, 280 mm TL; SU 66815, 8 females, 213, 216, 227, 229, 234, 246, 248, 260 mm TL, and 233 mm TL immature male; 29°33'N 88°38'W. CARIBBEAN SEA: ORE 3627, 4 adult males, 255, 270, 277, 278 mm TL, 16°50'N 81°21'W, off Jamaica; ORE 1870, 284 mm TL female, 16°39'N 82°29'W, off Honduras; SU 66814, 5 females, 206, 206, 215, 232, 250 mm TL, 2 immature males, 198, 205 mm TL, 3 adult males, 270, 273, 275 mm TL, 14°08'N 81°55'W, east of Cayos Miskito, Nicaragua. NO DATA: LJVC-0075, 315 mm TL adult female (cranium in Fig.13A); LJVC-0076, 319 mm TL adult female; LJVC-0077, 310 mm TL adult female; LJVC-0078, 315 mm TL adult female (2 skeletonised); RUSI 6105, 267 mm TL adolescent male, head dissected.

Galeus boardmani. AUSTRALIA: AMS IA2483, 542 mm TL adult male, HOLOTYPE of *Pristiurus (Figaro) boardmani* Whitley, 1928, Montague Island, NSW (radiographed); AMS I22807-020, 225 mm immature male, 252 mm female, 176 mm female, continental shelf of north-western Australia, 200 m; CSIRO H989.04, 432 mm adult male (skeletonised), SO5/84/63, 21 Oct. 1984, 43°41'S 145°46'E.

Galeus eastmani. JAPAN, Honshu: SU 7740, 336 mm TL female, Izu, HOLOTYPE of *Pristiurus eastmani* Jordan & Snyder, 1904; SU 35469, 344 mm TL adult male, Sagami Sea.

Galeus melastomus. EASTERN NORTH ATLANTIC: ISH 223/75, 472 mm TL adult female, 43°28'N 09°16'W; LJVC-0454, 680 mm TL adult female, south-west of Lousy Bank; SU 20604, 380 mm TL immature female, Naples, Italy.

Galeus murinus. EASTERN NORTH ATLANTIC: ISH 769/64, 530 mm TL adult female, 65°13'N 27°49'W; ISH 41/65, 495 mm TL adult male, 64°07'N 27°16'W.

Galeus polli. NAMIBIA: RUSI 6258, 215 mm TL immature female; SAM-29460, 311 mm TL adult female; SAM-uncat. 313 mm TL adult male and 339 mm TL adult female with 7 late fetuses, 5 males, 67-84 mm TL, 2 females, 80-86 mm TL. *Africana* A3439 039 E17, 390 mm female, (skeletonised, cranium as Fig.13H), 24°28.6'S 13°24.6'E, 308 m; SAM-uncat., *Africana* A8370 069 E17 (cancelled station), 291 mm TL adolescent male, 375 mm adult female, 23°19.1'S 13°9.9'E, 407 m. SAM-uncat., *Africana* cruise 069, aborted station (after A8397), 5 adult females, 350, 364, 375, 385, 390 mm TL, 25°50.9'S 13°9.9'E, 411 m. *Africana* A6948 059 E17, 311 mm TL late adolescent male, 4 adult males, 310, 317, 326, 329 mm TL, 4 females, 349, 361, 363, 387 mm TL, 27°31.6'S 14°31.3'E.

Galeus sauteri. TAIWAN: SU 21261, 4 adult males, 364, 367, 367, 370 mm TL, Takao, SYNTYPES of *Pristiurus sauteri* Jordan & Richardson, 1909; CAS Acc. 1971-VI: 11, 382 mm TL subadult female, CAS Acc. 1972-III: 14, 383 mm TL adult male and 450 mm TL adult female, all from Taiwan Straits; DAE 881605, 317 mm TL adolescent male, 169 mm immature male and 2 immature females, 110-131 mm, Tachi fish market. PHILIPPINE ISLANDS: CAS 34132, 2 females, 301-303 mm TL, Batangas Province, Batangas Bay, east of Talaga (identification provisional).

Galeus schultzi. PHILIPPINE ISLANDS, LUZON, BATANGAS

PROVINCE, BALAYAN BAY: CAS 33783, 177 mm TL female, south of Cape Santiago; CAS 34556, 2 immature males, 165-182 mm TL, south-east of Pagapas Bay; CAS 34852, 143 mm TL immature female and 155 mm TL immature male, south-east of Pagapas Bay; CAS 34861, 147 mm TL immature male, south of Cape Santiago.

Galeus gracilis n.sp.

Slender sawtail catshark

Figs 1-10, 13E

Type material. HOLOTYPE, CSIRO H1208.01, 335 mm TL adult female, Jan. 1988, upper slope north of Melville Island, NT, 9°49'S 130°15'E, 290 m.

PARATYPES, CSIRO CA3304, 317 mm TL adult female, SO2/82/45, 13 Apr. 1982, upper slope north of Dampier Archipelago, WA, 18°48'S 116°51'E, 403 m; CSIRO CA4477, SO1/84/17, 329 mm TL adult male, and CSIRO CA4478, 333 mm TL adult male (dissected), both from SO1/84/17, 31 Jan. 1984, upper slope north of Dampier Archipelago, WA, 18°41'S 117°04'E, 453 m.

Non-type material. QM 120676, 150 mm TL, 9°S 144°E; WAM 28098, 330 mm TL adult male, 1983, 18°44'S 116°59'E.

Diagnosis. *Galeus* with a long, parabolic snout, snout tip narrowly rounded. Preoral length about 6.4-7.8% TL and 0.9-1.0 times mouth width; prenarial snout 0.9-1.3 times eye length. Eyes dorsolateral on head, with narrow but well-developed subocular ridges. Eyes small, length 3.2-3.3% TL in adults; eye length 5.7-6.7 in head length. Mouth moderately large and long, broadly arched, width 7.0-8.1% TL. Labial furrows moderately long, not confined to mouth corners. Teeth

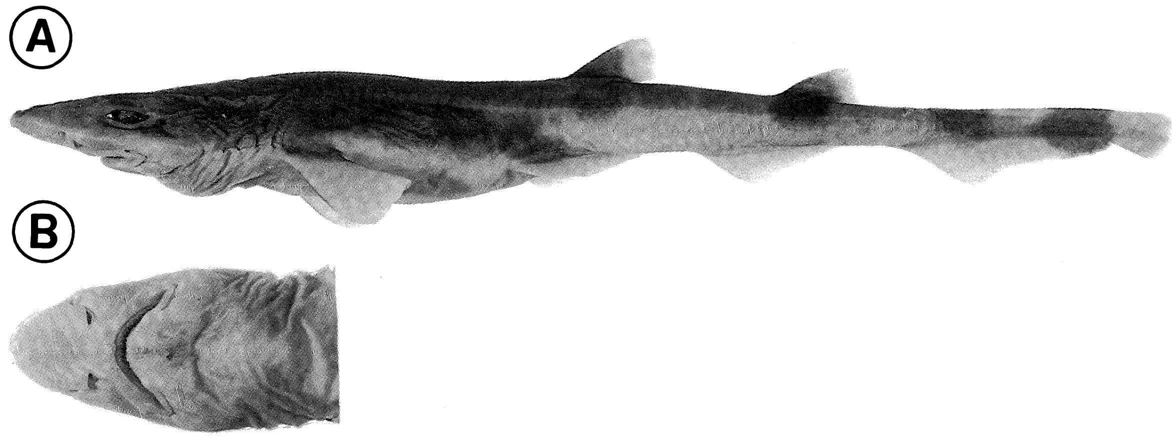

Fig.1. *Galeus gracilis* n.sp., CSIRO H1208.01, 335 mm TL adult female holotype. A, lateral view; B, underside of head, enlarged. Photos by T. Carter.

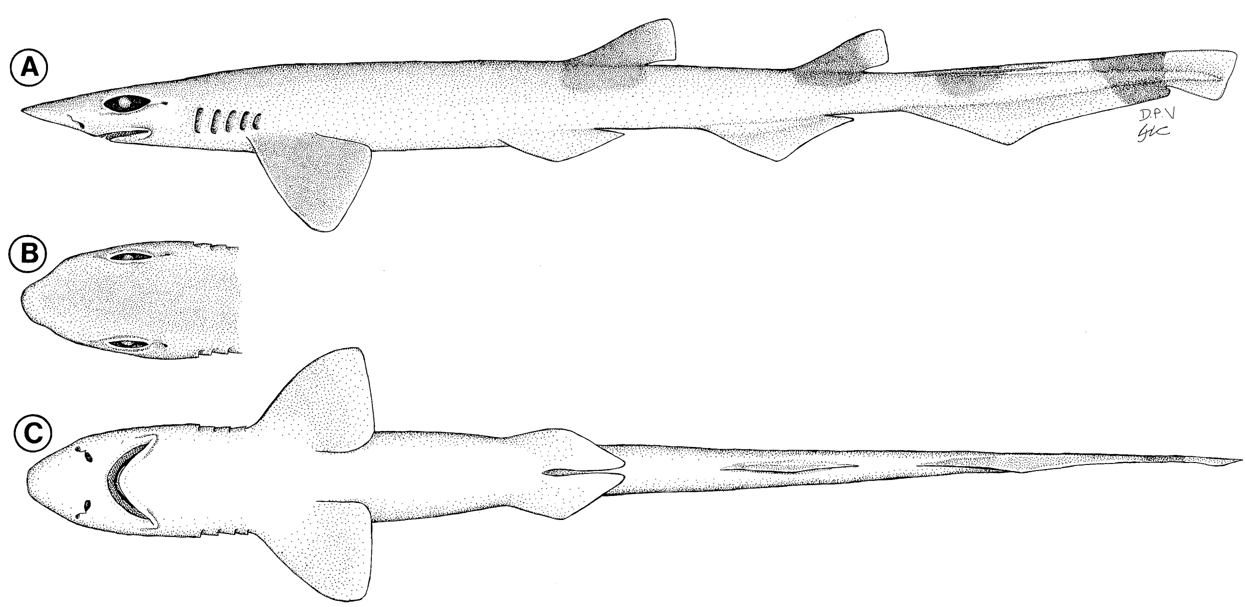

Fig.2. *Galeus gracilis*, CSIRO CA3304, 317 mm TL adult female paratype. A, lateral view; B, dorsal view of head; C, ventral view. Illustration by D. Voorfelt and L.J.V. Compagno.

in 54-57/54-62 rows. Body and precaudal tail slender. Caudal peduncle not greatly compressed, width 1.1-1.4 in height; peduncle elongated, anal-caudal space 0.5-0.7 of anal-fin base. Abdomen long, pectoral-pelvic space 14.3-16.0% TL and 0.7-0.9 of head length in adults. Pelvic-anal space long, 0.8-1.0 of anal base. Claspers moderately long in adult males, clasper outer length 10.3-10.8% TL, distal tips extending well behind pelvic fin rear tips but falling just short of anal-fin origin. Claspers tapering rearwards from base, not cylindrical or hourglass-shaped, tips narrow, pointed, not strongly twisted or truncated. Clasper tips with prominent groups of enlarged, anteriorly pointing hooked denticles on their lateral and mesial surfaces. Clasper glans very long, about 0.6 length of clasper from apopyle to tip. Cover rhipidion small but well developed. Pseudosiphon present and well developed. Exorhipidion large, bulbous, with group of enlarged, anteriorly pointing hooked denticles on outer lateral surface, but without transverse clasper hooks on mesial edge. Pectoral fin moderately large and broad, anterior margin 9.7-11.0% TL. Pectoral-fin skeleton with 16 radials; 2 proximal segments of mesopterygial radials fused together. Pelvic fins small, low, angular. Anal fin very short, base 10.5-11.5% TL and 1.1-1.2 in interdorsal space; anal origin under anterior half of interdorsal space; anal height 3.0-3.7 in base. No subcaudal crest of enlarged denticles on preventral caudal-fin margin. Total centra 130-134, MP centra 33-36, DP centra 41-44, precaudal centra 74-78. Intestinal valve with 6-7 turns. Chondrocranium with long rostrum, medial rostral cartilage 39% of NBL. Bases of lateral rostral cartilages narrow-spaced. Nasal capsules very large and obliquely elongated, anterior margins at approximately a right angle to each other. Anterior fontanelle small and nearly round, not longitudinally elongated. Cranial roof moderately broad and arched. Preorbital processes small. Suborbital shelves with nearly straight, posteriorly divergent edges. Postorbital processes small and directed anterolaterally. Otic capsules small. Occipital condyles prominently exserted. Size small, adults of both sexes 312-335 cm long. Mode of reproduction unknown. Adults light gray above, with well-defined dark saddles on body below first and second dorsal fins, on upper caudal fin base, and across caudal at base of terminal lobe, not highlighted with light lines; dorsal fins dusky with light distal webs; mouth lining blackish.

Etymology. From Latin *gracilis*, slender, gracile, in reference to the slim proportions of this little shark.

Description. Proportional dimensions as percentages

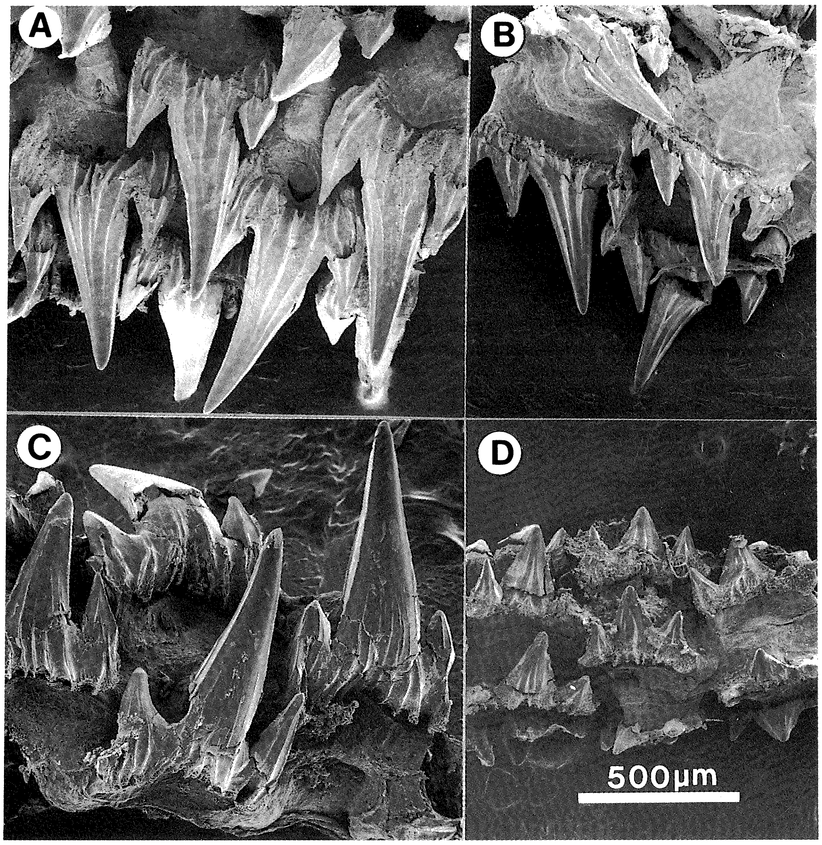

Fig.3. *Galeus gracilis*, scanning electron micrographs of groups of representative teeth from left side, labial views with roots imbedded in dental membrane, CSIRO CA4478, 333 mm TL adult male paratype. A-B, upper teeth; C-D, lower teeth. A, teeth from near upper symphysis; B, teeth from near end of upper dental band; C, teeth from near lower symphysis; D, teeth from near end of lower dental band. Scale bar (for all photographs) = 0.5 mm or 500 microns. Photos by A.J. Rees.

of total length for the holotype and 3 paratypes are presented in Table 1.

Head short, length 1.1 times pectoral-pelvic space. Head fairly narrow but strongly depressed, with a flat trapezodial cross-section at eyes. Outline of head in lateral view nearly straight or slightly convex in front of pectoral fins; in dorsoventral view head has a broad parabolic outline anterior to gill openings. Preoral snout 0.9-1.0 times mouth width, with a narrowly rounded tip in dorsoventral view, noticeably indented anterior to nostrils; snout bluntly pointed in lateral view, nearly straight or slightly convex above and below.

External eye opening with prominent anterior and posterior eye notches; eyes moderately large and spindle-shaped, eye length 5.7-6.7 in head length and 1.8-3.7 times eye height. Eyes dorsolateral on head, with lower edges distinctly medial to horizontal head rim in dorsal view, subocular ridges narrow but strong. Nictitating lower eyelids of rudimentary type, with shallow, scaled subocular pouches and secondary lower eyelids free from upper eyelids.

Spiracles small, length 2.8-5.5 in eye length, spiracles 0.2-0.4 eye lengths behind and below posterior eye notch. First 3 or 4 gill openings about equally high, fifth 0.4-1.2 height of third; third 9.4-23.6 in head and 0.3-0.6 of eye length. Gill openings straight to slightly concave, gill filaments not visible from outside. Upper ends of gill openings slightly below lower edges of eyes, gill openings not elevated on dorsolateral surface of head. No gill-raker papillae on gill arches.

Nostrils with small elongated incurrent apertures without posterolateral keels, small, bluntly angular anterior nasal flaps, small, low mesonarial flaps, large oval excurrent apertures, low posterior nasal flaps. Nostrils well in front of mouth, with anterior nasal flaps far in front of upper symphysis. Nostril width 1.0-1.3 in internarial space, 1.4 in eye length, 0.4-0.9 in third gill opening width.

Mouth broadly arched, moderately large and short, mouth width about 0.7 of head width at mouth corners, 2.5-3.1 in head length; mouth length 1.8-2.5 in mouth width. Lower symphysis falling short of upper symphysis, teeth prominently exposed in ventral view. Tongue moderate-sized, flat and rounded, filling most of floor of mouth. Maxillary valve narrow, width about 0.2 of eye diameter, highly papillose. No large buccal papillae on floor and roof of mouth behind maxillary valve. Palate with buccopharyngeal denticles confined to a crescent band covering its anterior third, denticles present on gill arches but absent from tongue and floor of pharynx behind tongue. Labial furrows moderately long, anterior ends of uppers well behind lower symphysis. Labial cartilages well developed.

Teeth in 57/62 (CSIRO CA3304), 54/54 (CSIRO CA4477), and 54/62 (CSIRO CA4478) rows in the 3 paratypes, 2-3/3-4 series functional. Teeth not arranged in diagonal files, no toothless spaces at symphysis. Teeth not highly differentiated in upper and lower jaws and along jaws, tooth row groups include medials (M) and anteroposteriors (AP). Tooth formula (CSIRO CA4478) is:

$$\text{Left}\ \frac{\text{AP27 M1 AP29}}{\text{AP30 M3 AP28}}\ \text{Right}$$

Sexual heterodonty present but weak, teeth slightly enlarged and with longer cusps in adult males. Height of upper anterolateral tooth near symphysis 0.37% of total length in adult male (CSIRO CA4477, 1.2 mm) but 0.22% in adult female (CSIRO CA3304, 0.7 mm). Upper teeth slightly narrower crowned and with longer transverse ridges than lowers near symphysis. Medials weakly differentiated at symphysis, slightly smaller than adjacent anteroposteriors. Anteroposteriors in both jaws have strong erect to semioblique (in upper posterior teeth) cusps and usually one strong high cusplet on either side. All teeth with strong basal ledges and grooves, strong transverse ridges notching

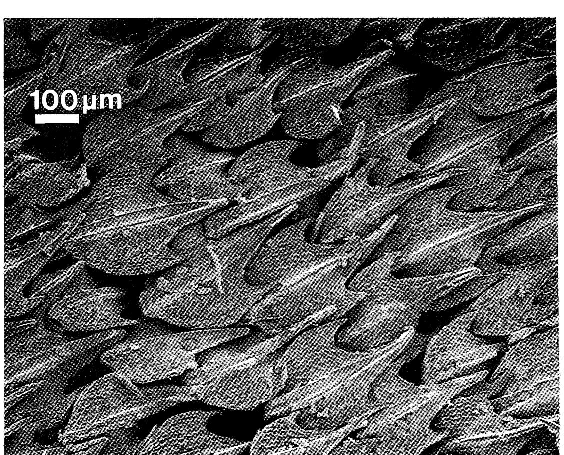

Fig.4. *Galeus gracilis*, scanning electron micrograph of lateral trunk denticles from back of CSIRO CA4478, 333 mm TL adult male paratype. Scale bar = 0.1 mm or 100 microns. Photo by A.J. Rees.

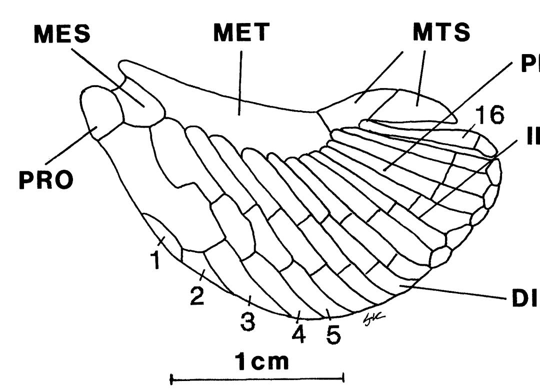

Fig.5. *Galeus gracilis*, pectoral fin skeleton from CSIRO CA4478, 333 mm TL adult male paratype. Numbers show convention for counting pectoral fin radials. This specimen has 16 radials, including one on the propterygium, three on the mesopterygium, and 12 metapterygial radials. Abbreviations: DIS – distal radial segments; INS – intermediate radial segments; MES – mesopterygium; MET – metapterygium; MTS – metapterygial segment (axis); PRO – propterygium; PRS – proximal radial segments. Illustration by L.J.V. Compagno.

basal ledges, extending onto cusps and cusplets partway to their tips, and low, flat roots. Gradient monognathic heterodonty well developed in anteroposterior teeth; distally anteroposteriors become smaller, with thicker and (in upper teeth) more oblique cusps, and lower cusplets. On most distal upper teeth cusp is shifted slightly distal on crown foot, with sometimes 2 mesial cusplets, but neither upper nor lower teeth are comb-shaped. Tooth histological type orthodont, with a definite pulp cavity.

Body slender, trunk vertically oval in section at first dorsal-fin base, length of trunk from fifth gill openings to vent 1.0-1.2 times head length. No predorsal, interdorsal or postdorsal ridges on midline of back, no postanal ridge between anal-fin base and lower caudal-fin origin; no lateral ridges on body. Caudal peduncle moderately long, low, slightly compressed, cylindrical-tapering and without lateral keels, caudal peduncle height at second dorsal-fin insertion 1.1-1.4 of width there, 0.9-1.4 in dorsal-caudal space.

Lateral trunk denticles with flat, elongated teardrop-shaped crowns about 1.6 times as long as wide, with all surfaces except medial ridges covered with prominent reticulated depressions. Crown with a strong single or narrow double medial ridge that extends entire length of crown onto the long, strong, narrow medial cusp; medial cusp about as long as the rest of the crown. Lateral cusps well developed, narrow, acute, and about a fourth as long as medial cusp, lateral ridges absent.

Pectoral fins broad and rounded-triangular, not falcate, with broadly convex anterior margins, broadly rounded apices, nearly straight posterior margins, broadly rounded free rear tips, convex inner margins, and broad bases. Pectoral-fin anterior margin 0.9-1.0 times pectoral-fin length. Pectoral fins nearly 3 times area of first dorsal fin. Origins of pectoral fins below fourth gill opening or below interspace between fourth and fifth gill openings. Apex of pectoral fin anterior to its free rear tip when fin is elevated and adpressed to body.

Pectoral fin skeleton with radials extending about 0.4 of pectoral anterior margin length into fin. Radials almost entirely divided into 3 segments, except for last metapterygial radial and possibly propterygial radial, which are bisegmental; longest distal segment 0.9 times length of its proximal segment. Pectoral-fin skeleton tribasal, propterygium probably with a single radial, mesopterygium probably with 3 radials, metapterygium

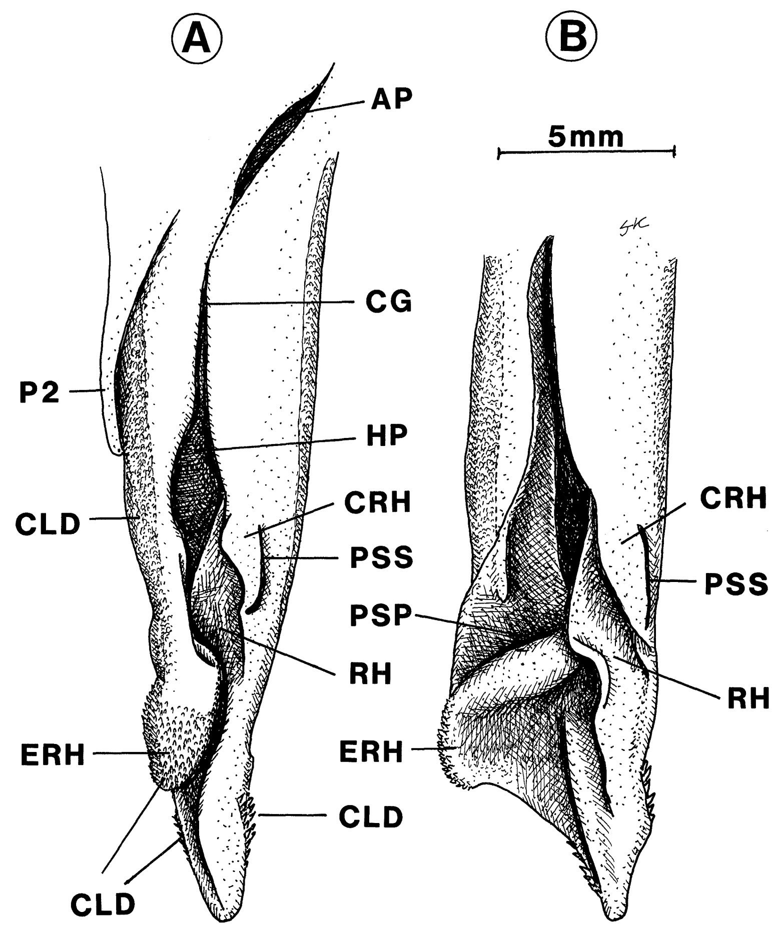

Fig.6. *Galeus gracilis*, left clasper in dorsal view from CSIRO CA4478, 333 mm TL adult male paratype. A, glans not dilated; B, glans spread. Abbreviations: AP – apopyle; CG – clasper groove; CLD – clasper denticles (including enlarged denticles on exorhipidion and clasper tip); CRH – cover rhipidion; ERH – exorhipidion; HP – hypopyle; P2 – pelvic fin; PSP – pseudopera; PSS – pseudosiphon; RH – rhipidion. Illustration by L.J.V. Compagno.

with 10 radials on basal segment, 2 on metapterygial axis; total radial count 16. Propterygium short, broad and subquadrate, not distally elongated. Proximal segments of propterygial radial and first mesopterygial radial forming a fused plate with intermediate segments of first and second mesopterygial radials. Mesopterygium and metapterygium not separated by an elongated fenestra. Mesopterygium short, subpentagonal, slightly elongated distally in the axes of its radials. Proximal segments of second and third mesopterygial radials fused together. Metapterygial basal segment triangular, elongated diagonal to the axes of its radials; metapterygial axis long, bisegmental, with length about 0.7 of metapterygial basal segment.

Pelvic fins low, broadly triangular; pelvic anterior margins 0.4-0.7 of pectoral-fin anterior margins; pelvic area slightly less than anal-fin area. Pelvic-fin anterior margins nearly straight or slightly convex, apices broadly rounded, posterior margins nearly straight, free rear tips attenuated and relatively pointed, inner margins not fused over claspers in adult males but with a slight fold of skin stretching between them.

Claspers relatively long but stout at base, convex and strongly tapering on lateral edge, clasper glans long and with slightly twisted, long, narrow tip. Claspers extending well behind pelvic-fin free rear tips in adult males but falling in front of anal-fin origin by only 0.2 of anal base. Most of dorsal surface of clasper naked except exorhipidion, and lateral and mesial margins; greatly enlarged clasper denticles with anteriorly directed cusps in two groups on mesial and lateral surfaces of clasper tip behind exorhipidion (HD2 and HD3 of Tachikawa & Taniuchi, 1987), these forming sawlike rows. Exorhipidion strongly differentiated, originating behind cover rhipidion, with a broad, blunt apex, moderately long base, and partly free posterior end. Exorhipidion covered with a third group of large, anteriorly directed denticles (HD1 of Tachikawa & Taniuchi, 1987) but lacking specialised clasper hooks. Pseudopera weakly developed below anterior end of exorhipidion and just behind posterior end of cover rhipidion, very shallow. No envelope present anterior to hypopyle. Rhipidion

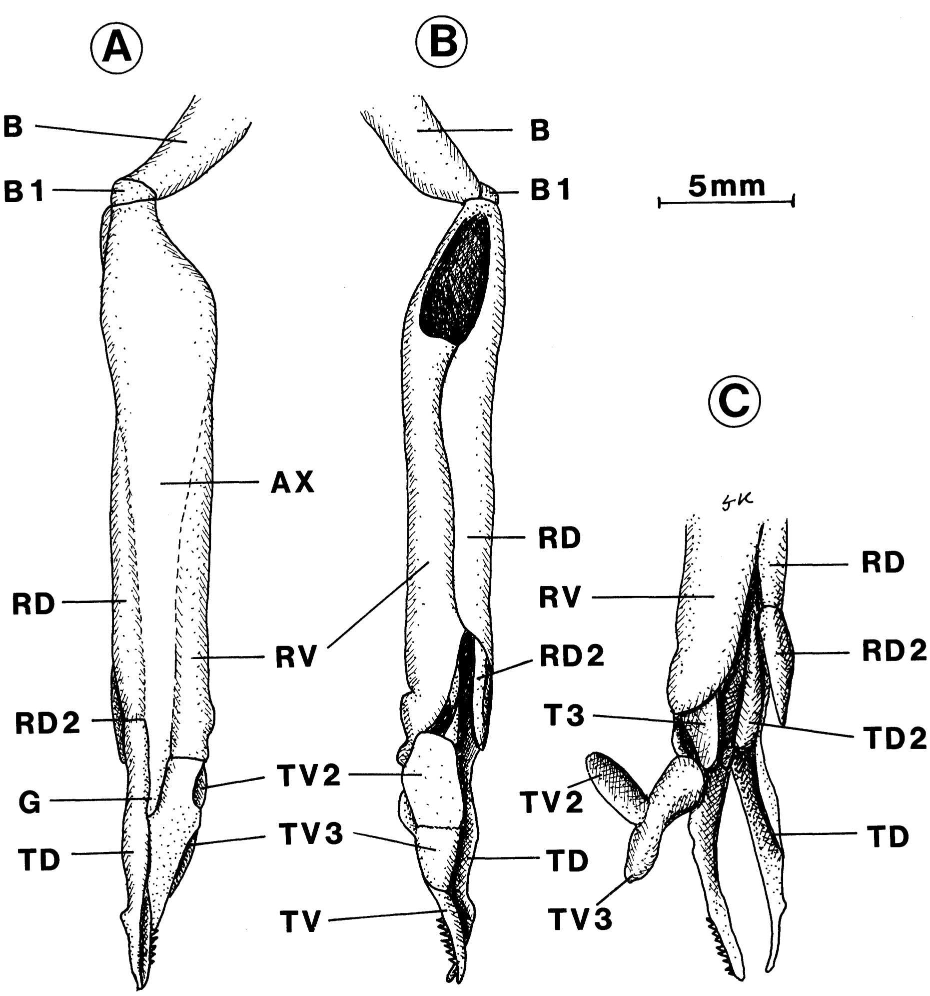

Fig.7. *Galeus gracilis*, clasper skeleton, CSIRO CA4478, 333 mm TL adult male paratype. A, ventral view; B, dorsal view, terminal cartilages not dilated; C, dorsal view of glans, terminal cartilages spread. Abbreviations: AX – axial cartilage; B – basipterygium; B1 – intermediate segment; G – end-style; RD – dorsal marginal cartilage; RD2 – accessory dorsal marginal cartilage; RV – ventral marginal cartilage; T3 – accessory terminal cartilage; TD – dorsal terminal cartilage; TD2 – dorsal terminal 2 cartilage; TV – ventral terminal cartilage; TV2 – ventral terminal 2 cartilage; TV3 – ventral terminal 3 cartilage. Illustration by L.J.V. Compagno.

present and large, extending over anterior two-thirds of clasper glans, formed as a flat, convex-edged blade with posterior end below apex of exorhipidion. Cover rhipidion greatly reduced, formed as a low lobe above anterior end of rhipidion, pseudosiphon short, narrow, slitlike, extending opposite most of the base of the cover rhipidion but not reaching exorhipidion. Apopyle and hypopyle connected by a long clasper groove, with its dorsal margins not fused in the specimens examined. Clasper siphons long and narrow, extending anterior to pelvic-fin bases about 0.9 of pectoral-pelvic space and nearly reaching pectoral-fin bases.

Clasper skeleton with almost all elements present. Axial cartilage or appendix-stem connected proximally by a single, very short basal segment (B1) to pelvic basipterygium, but with no apparent beta cartilage. Clasper shaft, formed from axial cartilage and tightly rolled dorsal and ventral marginal cartilages, moderately slender, forms a flattened cylinder extending to clasper glans. Clasper glans skeleton comprises a large, narrow, curved, hooked, spear-tipped dorsal terminal and more distally expanded ventral terminal with enlarged clasper denticles strongly anchored to its tip, articulating with and separated along their proximomesial third to short, narrow, cylindrical end-style (terminal extension of axial cartilage); elongated, mesially twisted posterior ends of terminal cartilages separated by a narrow gap. Accessory dorsal marginal cartilage (RD2) is a long, wedge-shaped, distally tapering cartilage that supports the weak cover rhipidion. Accessory dorsal terminal cartilage (TD2) is a small, elongated, blade-like, distally expanded cartilage that extends along anterior end of clasper glans from dorsal marginal nearly to tip of abbreviated end-style, supports rhipidion. Accessory ventral terminal cartilages (TV2 and TV3) support exorhipidion, consist of a posteriorly tapering, thick TV3 cartilage that articulates anteriorly with a lateral projection of the TV, and an elongated, subrectangular TV2 cartilage that articulates with anterolateral end of TV3, extends anteriorly to barely reach the distal end of the ventral marginal. A short, broad, wedge–like accessory terminal cartilage (T3) opposite the TD2 cartilage is proximally sheathed by terminal extension of ventral marginal. T3 cartilage ends well anterior to TV3-TV articulation.

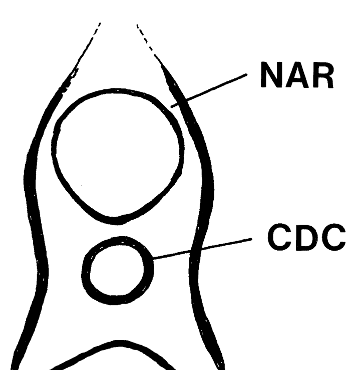

Fig.8. *Galeus gracilis*, vertebral calcification pattern, CSIRO CA4478, 333 mm TL adult male paratype. Abbreviations: CDC – calcified double cone; NAR – neural arch. Illustration by L.J.V. Compagno.

First dorsal fin low, narrow at apex and not falcate, with slightly undulating or convex anterior margin, bluntly angular apex, slightly convex posterior margin, abruptly angular free rear tip, and slightly concave inner margin. First dorsal-fin origin about opposite midbases of pelvic fins, midpoint of dorsal-fin base about opposite pelvic-fin insertions, insertion about equidistant between anal-fin origin and pelvic-fin insertions or 1.5 times closer to pelvic fins, free rear tip about inner margin length anterior to anal-fin origin. Posterior margin nearly vertical, insertion well anterior to dorsal apex. First dorsal-fin base 1.7-2.3 in interdorsal space, 3.3-4.5 in dorsal caudal-fin margin; first dorsal-fin height 1.1-2.0 in first dorsal-fin base; first dorsal-fin inner margin 1.4-2.3 in first dorsal-fin height, 2.4-3.0 in first dorsal-fin base.

Second dorsal fin low, narrow at apex and not falcate, about 0.9 of first dorsal-fin area, second dorsal-fin height 0.7-0.9 of first dorsal-fin height, base 0.7-1.0 of first dorsal-fin base. Second dorsal fin with nearly straight anterior margin, bluntly angular apex, straight posterior margin, broadly angular free rear tip, nearly straight or slightly convex inner margin. Second dorsal-fin origin about opposite last third of anal-fin base, insertion slightly in front to slightly behind anal-fin free rear tip, free rear tip above or just in front of upper caudal-fin origin. Posterior margin slanting posteroventrally from apex, insertion well anterior to dorsal apex. Second dorsal-fin base 0.5-0.7 in dorsocaudal space, second dorsal-fin height 1.5-1.7 in second dorsal-fin base, second dorsal-fin inner margin 1.4-1.6 in second dorsal-fin height and 2.3-2.5 in second dorsal-fin base.

Anal fin low, narrow at apex, not falcate, and at least twice the area of second dorsal fin, anal-fin height 0.8-1.0 in second dorsal-fin height and base 1.9-2.1 times second dorsal-fin base. Anal-fin anterior margin nearly straight or slightly undulated, apex rounded, posterior margin slightly concave, free rear tip acutely pointed, and inner margin straight. Anal-fin base without preanal ridges, anal-fin origin 0.7-0.9 of its base length behind pelvic-fin insertions, free rear tip 3.0-3.6 times anal-fin inner margin anterior to lower caudal-fin origin. Anal-fin posterior margin slanting posterodorsally, anal-fin insertion far behind apex. Anal-fin base 0.5-0.7 in anal-caudal space, anal-fin height 3.0-3.7 in anal-fin base, anal-fin inner margin 1.8-2.0 in anal-fin height and 5.5-7.4 in anal-fin base.

Caudal fin very narrow-lobed and asymmetrical, with large terminal lobe and ventral lobe hardly developed. Caudal fin elongated, dorsal margin 2.6-3.0 in precaudal length. Preventral caudal-fin margin 2.7-3.3 in dorsal caudal-fin margin, terminal lobe 4.7-4.8 in dorsal caudal-fin margin, subterminal margin 0.8-1.1 in terminal margin. Dorsal caudal-fin margin slightly undulated above, without lateral undulations, preventral margin basally concave and apically straight, tip of ventral caudal-fin lobe broadly angular, upper and lower postventral margins not differentiated, postventral margin broadly concave, subterminal notch a narrow, deep slot, subterminal margin nearly straight, terminal margin straight to convex, lobe formed by these margins angular, and tip of tail angular.

Total vertebral counts (TC) 130-134, monospondylous precaudal (MP) centra 33-36, diplospondylous precaudal (DP) centra 41-43, precaudal (PC) centra 74-78, and diplospondylous caudal (DC) centra 55-56. MP counts 26.1-26.8%, DP counts 31.3-31.5%, and DC counts 41.7-42.3% of TC counts. Ratios of DP/MP counts 1.2, DC/MP counts 1.6, 'A' ratio 133-146, 'B' ratio 86-133 (see Table 2 for detailed count data and ratios). Transition between MP and DP centra well behind pelvic origins and over rear ends of pelvic bases, about 5 or 6 centra

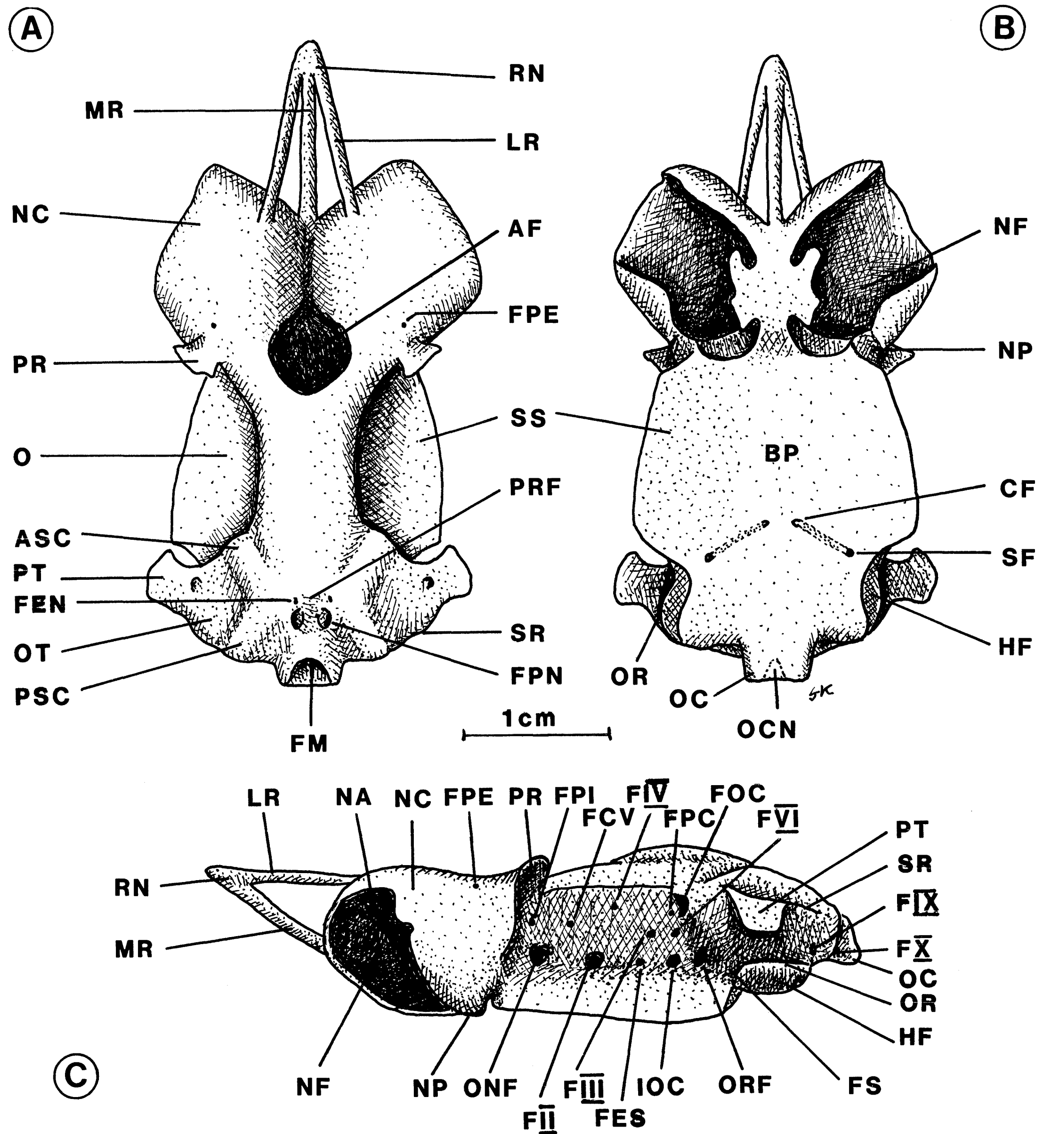

Fig.9. *Galeus gracilis*, chondrocranium from CSIRO CA4478, 333 mm TL adult male paratype. A, dorsal; B, ventral; C, lateral views. Abbreviations: AF – anterior fontanelle; ASC – anterior semicircular canal; BP – basal plate; CF – internal carotid foramen; FCV – foramen for anterior cerebral vein; FEN – endolymphatic foramen; FES – foramen for efferent spiracular artery; FM – foramen magnum; FOC – foramen for superficial opthalmic nerve; FPC, FPE and FPI – cranial, external and orbital foramina of deep ophthalmic nerve; FPN – perilymphatic foramen; FII – optic nerve foramen; FIII – oculomotor nerve foramen; FIV – trochlear nerve foramen; FVI – abducens nerve foramen; FIX – glossopharyngeal nerve foramen; FX – vagus nerve foramen; HF – hyomandibular facet; IOC – interorbital canal; LR – lateral rostral cartilage; MR – medial rostral cartilage; NA – nasal aperture; NF – nasal fontanelle; NC – nasal capsule; NP – orbital notch; O – orbit; OC – occipital condyle; OCN – occipital centrum; ONF – orbitonasal foramen; OR – opisthotic ridge; ORF – orbital fissure; OT – otic capsule; PR – preorbital process; PRF – parietal fossa; PSC – posterior semicircular canal; PT – postorbital process; RN – rostral node; SF – stapedial foramen; SR – sphenopterotic ridge; SS – suborbital shelf. Illustration by L.J.V. Compagno.

behind pelvic girdle. Last few MP centra before MP-DP transition moderately enlarged, not forming a 'stutter zone' of alternating long and short centra. Diagonal calcifications absent from vertebral centra; intermedialia very weakly calcified and hardly indented medially.

Intestinal valve of conicospiral type, 2 specimens counted with 6 and 7 turns.

Chondrocranium (Fig.9) with elongated, slender, cylindrical rostral cartilages, these not hypercalcified and united at their distal tips into a short, unfenestrated rostral node. Medial rostral cartilage approximately 39% of NBL, distance between bases of lateral rostral cartilages 2.5 in medial rostral cartilage. Nasal capsules large, high, diagonally oval, slightly longer than wide, width across them 71% of NBL, length of capsule 0.9 in its width. Anterior margins of nasal capsules nearly straight, slanted obliquely at approximately a right angle to each other. Nasal apertures large, on anterolateral faces of capsules, separated from large nasal fontanelles by a broad channel. Ectethmoid chambers inside nasal cavities, at posterior edges of nasal fontanelles and not visible ventrally. Subnasal plate in the form of narrow medial extensions of the lateral capsule wall, butterfly wing-shaped lateral extensions of the narrow, high internasal septum bordering the nasal fontanelles. Prominent groove or channel on dorsal surface of nasal capsules on midline between anterior fontanelle and base of medial rostral cartilage. Small external profundus nerve foramina on posterodorsal surface of nasal capsules just anterior to bases of preorbital processes. Anterior fontanelle subrhomboidal and small, width about 1.1 times in its length and about 18% of NBL. Dorsal lip of fontanelle flat, without an epiphysial foramen. Cranial roof arched between orbits, well elevated above level of postorbital processes and forming a low flat dome above the posterior half of the orbits. Parietal fossa small, narrow, and moderately deep. Orbital notches relatively deep. Basal plate flat from orbital notches to occipital centrum, without keels. Internal carotid foramina about one-third as far from each other than from the stapedial foramina on either side of them. Supraorbital crests absent, with a low angular ridge connecting the bases of the preorbital and postorbital processes. Preorbital processes low, prominent, trapezoidal, laterally expanded, and obliquely elevated almost to dorsalmost dome of cranial roof. Postorbital processes broad-based, flat, angled anteriorly in dorsal view and ventrally in lateral view; distal blade of processes slightly expanded, with broadly convex lateral edge. Small foramen present at base of each postorbital process. Width across preorbital processes 55% of NBL, width across postorbital processes 66% of NBL. Orbits horizontally subrectangular in lateral view, with contents indicated in Figure 9C. Weak ledge between suborbital shelves and nasal capsules. Suborbital shelves arcuate-angular in shape, with edges deflected ventrally in lateral view and diverging posteriorly in dorsoventral view; shelves not expanded laterally to distal ends of the postorbital processes in dorsal view. Suborbital shelves relatively narrow, width across them 63% of NBL. Otic capsules not greatly expanded or inflated, their lengths about 30% of NBL and greatest width across them 48% of NBL. Sphenopterotic ridges low, posteriorly convergent, without pterotic horns. Opisthotic ridges low, not extending laterally to edges of sphenopterotic ridges. Hyomandibular facets small, horizontally oval, extending across middle third of otic capsules, not exserted posteriorly. Occipital condyles narrow, prominently exserted from occiput, with a single occipital centrum between them.

Colour in alcohol light gray-brown above, lighter below, back and upper surface of pectoral fin darker, anal fin, subterminal caudal web and terminal caudal-fin lobe dusky but with light margins, bases and proximal webs of dorsal fins dark but with light posterior margins. Bold dark gray-brown saddle-marks on base of precaudal tail below first dorsal-fin base, below second dorsal-fin base, at dorsal base of caudal fin just behind origin, and as a vertical band anterior to subterminal notch of caudal fin and delimiting the light terminal caudal-fin lobe. No dark blotch on hypaxial caudal-fin lobe. Saddle marks without light margins. In some specimens a broad, poorly defined dark blotch extends on sides and back from over pectoral fins to just in front of pelvic-fin bases. No small dark or light spots on fins or body. Inside of mouth dark gray or blackish.

Weight of H1208.01 (335 mm female holotype) is 116 gm; 2 adult male paratypes weigh 79 gm (CA4477, 329 mm) and 70 gm (CA4478, 333 mm).

Mode of reproduction. Unknown.

Distribution. At present *Galeus gracilis* is known from the northwestern continental slope off Western Australia and the Northern Territory (Fig.10), on the bottom at depths from 290 to 453 m.

Bessednov (1969) recorded two specimens of *Galeus eastmani* from the Gulf of Tonkin off Vietnam at 40 m depth. Springer (1979) and Compagno (1984, 1988) accepted this record, but Bessednov's *Galeus* may be closer to *G. gracilis* than *G. eastmani*. The specimen illustrated, a 331 mm female (Bessednov's, fig. 11; also included here as Fig.11), agrees with *G. gracilis* in its longer preorbital snout, smaller eye, and more boldly marked saddles, but agrees with *G. eastmani* as described by Nakaya (1976) in having dark blotches on the hypaxial and terminal caudal fin lobes (absent in *G. gracilis*). We consider the assignment of Bessednov's specimens to *G. eastmani* as questionable pending their reexamination.

Comparison with Other Species

The traditional external morphology and morphometrics, colouration and vertebral counts used in Springer's (1979) review of the genus *Galeus* has been supplemented by the work of Nakaya (1976), Muñoz-Chapuli & Ortega (1985), Tachikawa & Taniuchi (1987), and Compagno (1988). The morphological character systems they demonstrated to elucidate the systematics and interrelationships of the genus include: the detailed external morphology and anatomy of the claspers; the chondrocranial morphology; the denticle and dental morphology as revealed by the scanning electron microscope; the morphology of the pectoral fin skeleton. While such work points to the feasibility of elucidating the cladistic relationships of *Galeus*, several species are at present incompletely known in crucial character systems, particularly the chondrocranium, claspers and pectoral fin skeleton. There are linked problems with the monophyly and composition of *Galeus*, with its interrelationships with other galeine genera, and with lack of knowledge of some character systems in other galeines (see Compagno, 1988). This would make a cladistic

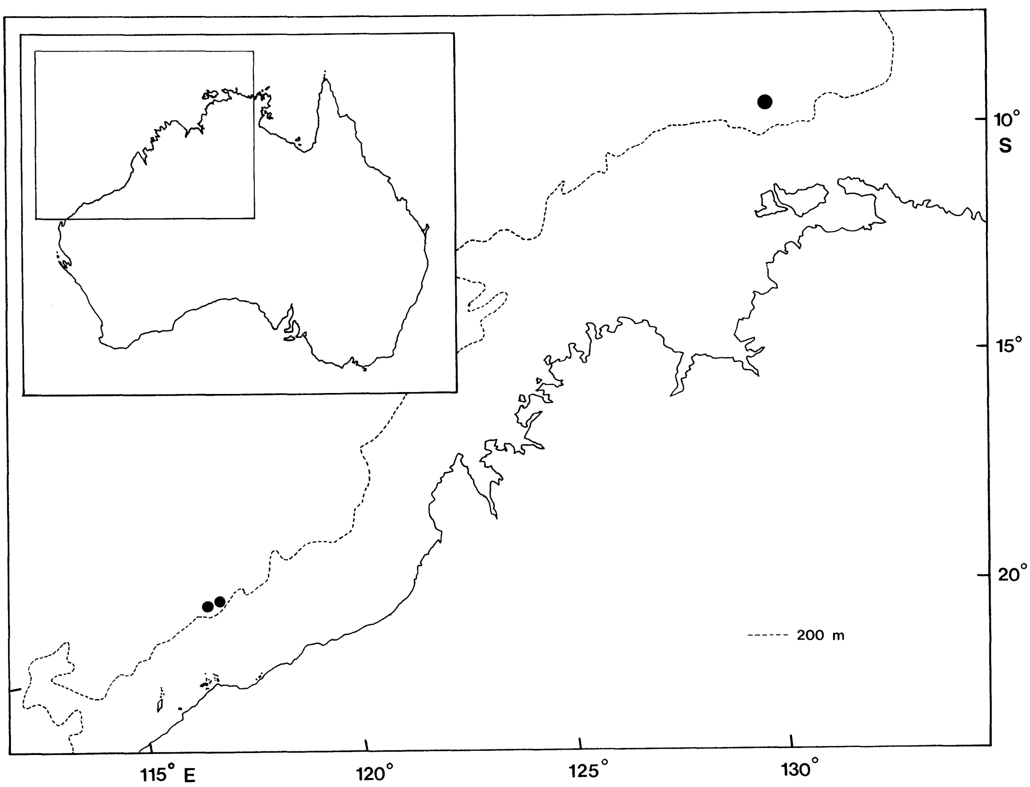

Fig.10. *Galeus gracilis*, distribution map. Inset: Australian continent with known range on North West Shelf circumscribed by square. Main map: enlargement of inset square with records of type specimens shown as black dots. Map by P. White.

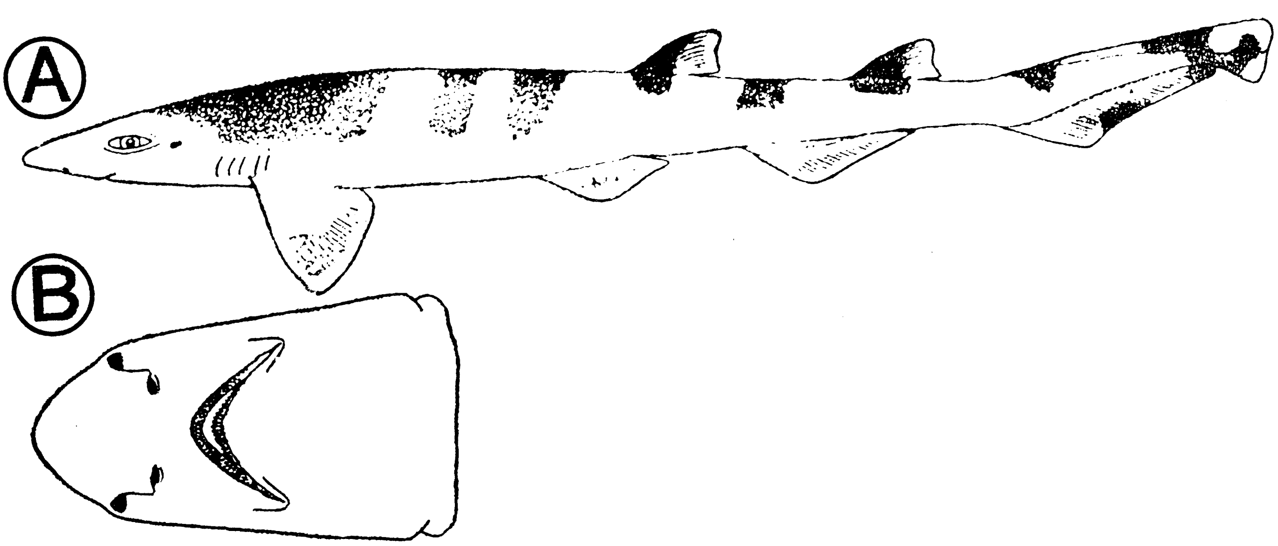

Fig.11. '*Galeus eastmani*' from the Gulf of Tonkin, Vietnam. A, lateral view of a 331 mm TL female; B, underside of head, enlarged. From Bessednov (1969).

analysis of *Galeus* premature.

For the descriptive purposes of this paper, other species of *Galeus* are compared and contrasted with *G. gracilis* without attempting a cladistic analysis. *Galeus gracilis* may be closest to *Galeus eastmani*, *G. longirostris*, and *G. nipponensis* from Japan; all four species have a relatively slender body, long precaudal tail, caudal peduncle not greatly compressed, and a relatively small anal fin. *Galeus gracilis* appears to be more distant from *G. sauteri* and *G. schultzi* from the western North Pacific and is not close to the *Asymbolus*-like *G. boardmani* from Australia (see Compagno 1988). *Galeus gracilis* is not close to eastern Pacific or Atlantic members of *Galeus*.

Galeus eastmani. *Galeus gracilis* most closely resembles the small *G. eastmani* in general morphology, size (adult *eastmani* to 395 mm TL) and in its similar tooth row, MP vertebral, and intestinal valve counts. *Galeus eastmani* as characterised from the study material and Nakaya's (1976) detailed account differs from *G. gracilis* in having a slightly shorter snout (POR 5.8-6.6% TL versus 6.4-7.8% TL for *G. gracilis*); more laterally situated, larger eyes in adults (EYL 3.5-4.2% TL versus 3.2-3.3% TL); possibly shorter anal-caudal space (ACS 0.2 of ANB versus 0.5-0.7); more strongly twisted, bent, bluntly pointed clasper tips (Fig.12A-B); a larger, more angular exorhipidion; a shorter clasper glans (0.4 of distance from apopyle to clasper tip versus 0.6 in *G. gracilis*); a vestigial cover rhipidion (well developed in *G. gracilis*); pseudosiphon absent; a slightly larger pectoral fin (P1A 10.6-13.4% TL versus 9.7-11.0); three fused proximal mesopterygial radial segments (2 in *G. gracilis*); a longer anal fin (ANB 12.6-15.2% TL versus 10.5-11.5); a less bold colour pattern of obscure saddles, but with dark markings on the hypural and terminal caudal fin lobes (absent in *G. gracilis*); more diplospondylous precaudal vertebrae (49-50 versus 41-44).

The chondrocranium of *G. eastmani* (Fig.13D) differs from that of *G. gracilis* in having much shorter rostral cartilages; a broader rostral node; more widely spaced bases on its medial rostral cartilages (distance between bases 1.4 times anterior fontanelle width versus 0.9 in *G. gracilis*); broader nasal capsules (width across capsules 1.4 *x* width across postorbital processes versus 1.0); a broader anterior fontanelle; parallel rather than posteriorly divergent edges on its suborbital shelves; lower postorbital processes; possibly lower occipital condyles.

Galeus boardmani. The little-known *Galeus boardmani* is the only other *Galeus* or *Galeus*-like galeine known from Australia. It resembles *G. gracilis* in its slender proportions, small fins, and dorsolateral eyes, but is otherwise quite distinct. It is compared in detail with *G. gracilis* here.

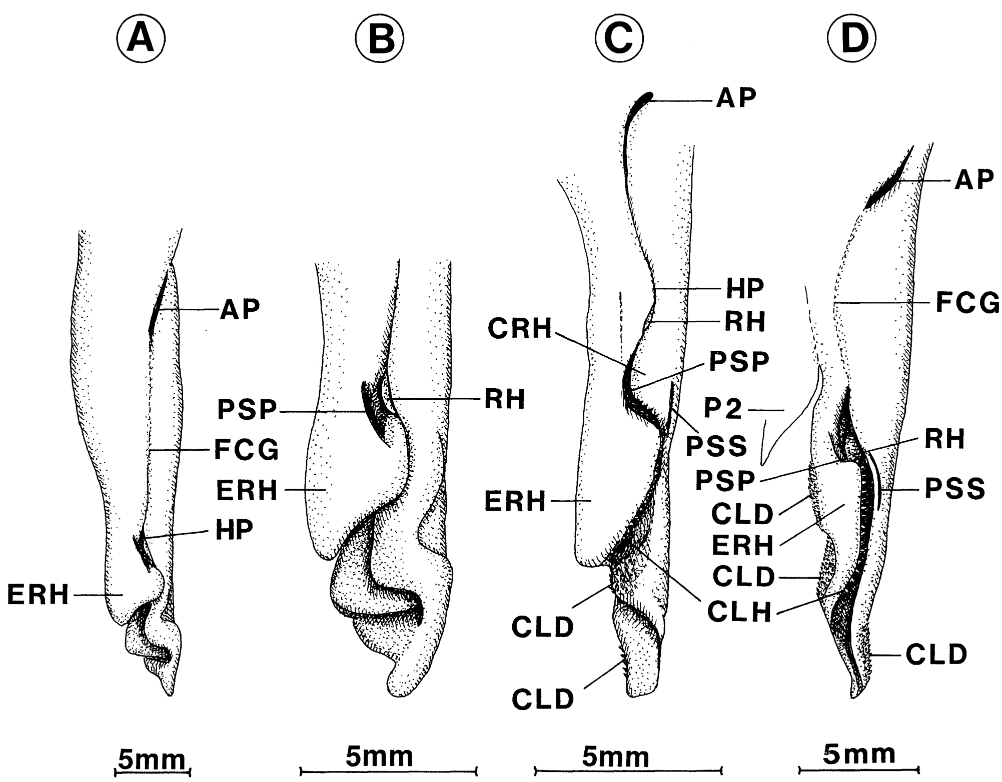

Fig.12. Left claspers of adult males of three species of *Galeus* in dorsal view. A-B, *Galeus eastmani*, SU-35469, 344 mm TL. A, entire clasper; B, enlarged view of clasper glans; C, *Galeus arae*, SB 2420, 305 mm TL, entire clasper; D, *Galeus polli*, RV *Africana* A6948 059 E17, 326 mm TL, entire clasper. Scale bars = 5 mm. Abbreviations as in Figure 6, except for CLH – clasper hooks (on medial edge of exorhipidion); FCG – fused clasper groove.

Galeus boardmani is provisionally assigned to *Galeus* but may be closer to members of the genus *Asymbolus* (Compagno, 1988). As characterised from specimens and from Whitley's (1928, 1940) accounts, *G. boardmani* grows much larger (adults to 610 mm TL) and has a broader, blunter, shorter snout (POR 0.8 of MOW versus 0.9-1.0 in *G. gracilis*); more elongated anterior nasal flaps and larger posterior nasal flaps; larger eyes in adults (EYL 4.3% TL and 4.0 in HDL versus 3.2-3.3% TL and 5.7-6.7% TL); more tooth rows in adults (67/74 versus 54-57/54-62); possibly a longer precaudal tail (distance from front of vent to dorsal caudal-fin origin approximately 37% TL versus 30.4-35.6% TL); pelvic-fin inner margins partly united as a low 'apron' of skin over claspers in adult males; a more erect first dorsal fin, with a less oblique anterior margin; possibly a longer interdorsal space (1.5 times the anal-fin base versus 1.1-1.2); a long, low ridge the underside of the caudal peduncle, and a row of enlarged, sawlike denticles on the ridge and the preventral caudal-fin margin (absent in *G. gracilis*); a shorter caudal fin (DCM in adults about 22% TL versus 25.4-27.9% TL); more numerous dark saddle markings (12-13 versus about 4) with conspicuous light edges (absent in *G. gracilis*); a light mouth (dark in *G. gracilis*); more numerous vertebrae, including DP counts (58 versus 41-43), PC counts (95 versus 74-78), and total counts (148 versus 130-134); more numerous intestinal valve turns (11 versus 6-7).

The claspers of *G. boardmani* and *G. gracilis* are somewhat similar in being relatively short, thick at the base, and gradually tapering, but there are numerous differences: those of *G. boardmani* are shorter (6.9% TL versus 10.3-10.8% TL) and have a shorter glans (Fig.14) about 0.5 of the distance from the apopyle to clasper tip (0.6 in *G. gracilis*); a well-developed clasper envelope (vestigial or absent in *G. gracilis*); a small, low bilobate

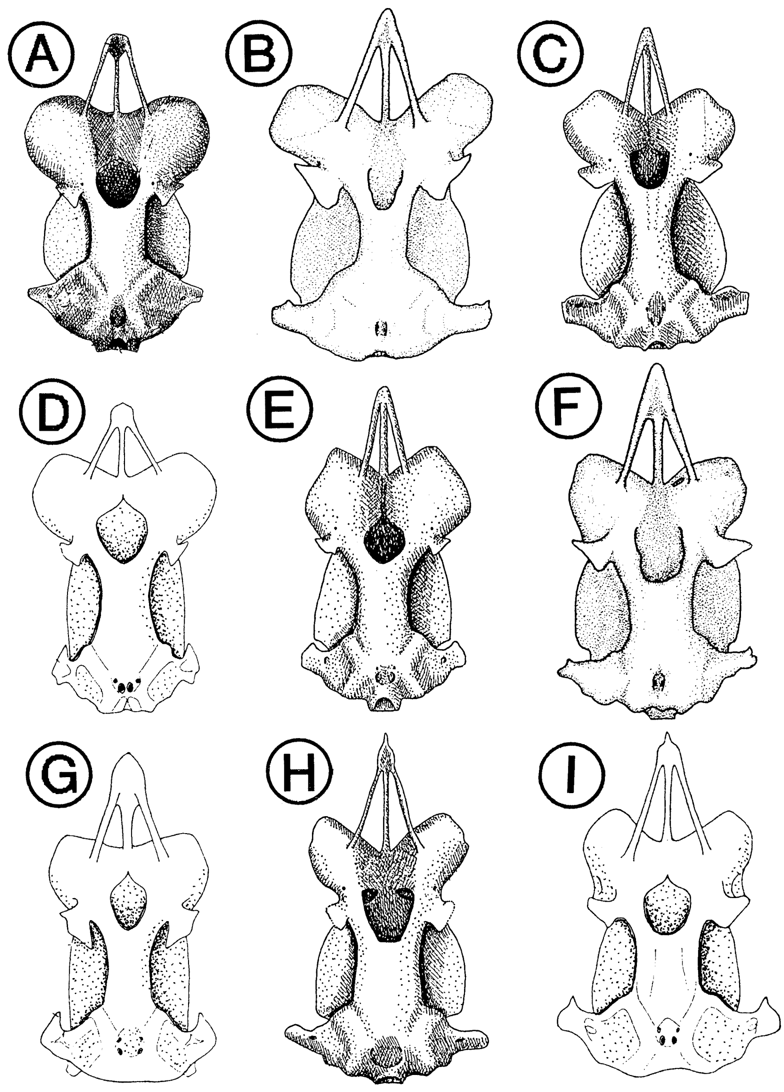

Fig.13. Chondrocrania from nine species of *Galeus* in dorsal view, adjusted to same nasobasal length (NBL). A, *G. arae*; B, *G. atlanticus*; C, *G. boardmani*; D, *G. eastmani*; E, *G. gracilis*; F, *G. melastomus*; G, *G. nipponensis*; H, *G. polli*; I, *G. sauteri*. A,C,E,H – illustrations by L.J.V. Compagno. A – modified from Compagno (1988); B,F – from Munoz-Chapuli & Ortega, 1985; D,G,I – modified from Nakaya (1976).

exorhipidion without a free posterior end (enlarged and bulbous, and with a free posterior end in *G. gracilis*); no enlarged anteriorly directed denticles on the exorhipidion, mesial, and lateral tips of the claspers (present in *G. gracilis*); a larger cover rhipidion that partly conceals the rhipidion; clasper tips not twisted (moderately twisted in *G. gracilis*).

The clasper skeletons of *G. boardmani* and *G. gracilis* have a full complement of clasper cartilages except for the beta cartilage, but differ markedly in the morphology of these cartilages. *Galeus boardmani* has broader dorsal and ventral marginals (Fig.15); a broader, less tapering axial cartilage; a longer appendix-stem over half the length of the ventral terminal cartilage; much smaller ventral terminal 2 and 3 cartilages (TV2 and TV3), reflecting its small exorhipidion; a larger, more hooked accessory terminal cartilage (T3; wedge-shaped in *G. gracilis*); a broader dorsal terminal 2 (TD2) cartilage; a smaller, more truncated accessory dorsal marginal (RD2) cartilage; the dorsal terminal cartilage much shorter and smaller than the ventral terminal cartilage (equal-sized and equally long in *G. gracilis*); the dorsal and ventral terminals without twisted tips (present in *G. gracilis*).

The chondrocranium of *G. boardmani* (Figs 13C,15) is generally similar to that of *G. gracilis* but differs in having shorter nasal capsules; smaller nasal fenestrae; narrower-based, broader lateral extensions of the internasal plate; a more U-shaped anterior fontanelle; a narrower cranial roof with the section anterior to the optic nerve foramen flat (arched above the orbits in *G. gracilis*); higher, larger orbits; larger, more dorsally elevated preorbital processes; broader, more posteriorly divergent and convex suborbital shelves; more laterally directed postorbital processes; shorter, higher hyomandibular facets; lower occipital condyles.

***Galeus longirostris* and *G. nipponensis*.** The two Japanese species *G. longirostris* and *G. nipponensis* as characterised by Nakaya (1976), Springer (1979) and Tachikawa & Taniuchi (1987) are similar to *G. gracilis* in their relatively long prenarial snouts (PRN 0.9-1.5 times EYL), dorsolateral eyes, long abdomens (PPS 12.7-16.5% TL), short anal fins (ANB less than 13% TL), and a long interdorsal space relative to the anal-fin base (IDS 1.0-1.5 times ANB). These species differ from *G. gracilis* in attaining a much greater size at maturity (adults 660-803 mm TL in *G. longirostris* and 530-656 mm TL in *G. nipponensis*) and in having much longer claspers (CLO at least 11.0% TL versus 10.3-10.8% TL in *G. gracilis*) that extend behind the anal-fin origin (not reaching it in *G. gracilis)*; cylindrical shafts and broad, strongly twisted tips on the claspers; clasper glans less than 0.5 of distance from apopyle to clasper tip (0.6 in *G. gracilis*); a vestigial cover rhipidion; darker dorsal colouration, with saddle markings irregular or absent in adults; white to gray-white mouths (blackish in *G. gracilis*); more MP centra (MP 37-40 in *G. nipponensis*, 40-45 in *G. longirostris* versus 33-36).

Galeus longirostris additionally differs from *G. gracilis* in its longer snout (POR 7.9-8.3% TL versus 6.4-7.8% TL); more broadly rounded snout tip; slightly larger eyes

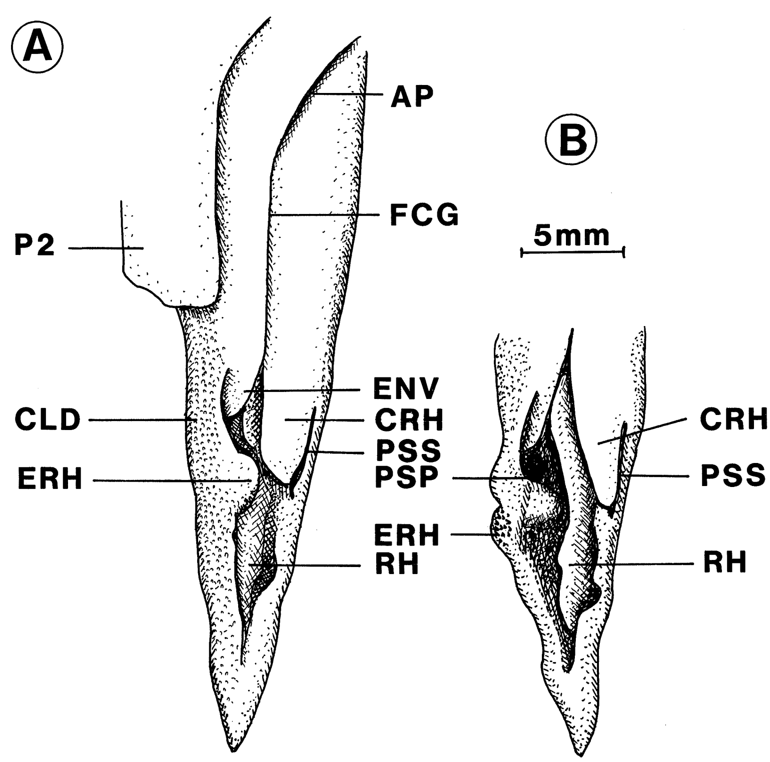

Fig.14. *Galeus boardmani*, left clasper in dorsal view from CSIRO H989.04, 432 mm adult male. A, glans not dilated; B, glans spread. Abbreviations as in Figure 6, except for FCG – fused clasper groove. Illustration by L.J.V. Compagno.

in adults (EYL 3.4-4.0% TL versus 3.2-3.3% TL); more broadly arched mouth; slightly longer labial furrows (2.1-2.5% TL versus 1.6-2.1% TL); slightly shorter caudal peduncle (ACS/ANB ratio 0.3-0.5 versus 0.5-0.7); larger pectoral fins (P1A 11.2-12.6% TL versus 9.7-11.0% TL); more numerous PC vertebral counts (91-97 versus 74-78).

Galeus nipponensis additionally differs from *G. gracilis* in its higher pectoral-fin radial counts (19 versus 16) and three fused proximal radials on the mesopterygium (2 in *G. gracilis*).

All three species have enlarged, anteriorly directed groups of denticles on the mesial and lateral faces of the clasper tip, but they are more prominent and numerous in *G. gracilis* than in *G. nipponensis*, but less numerous than in *G. longirostris*.

The chondrocranium of *G. longirostris* was not available for study, but that of *G. nipponensis* (Fig.13G) differs from that of *G. gracilis* in having thicker rostral cartilages; more widely spaced bases on the lateral rostral cartilages (distance between bases 1.7 times the anterior fontanelle width in *G. nipponensis*, 0.9 in *G. gracilis*); a much larger rostral node; smaller nasal capsules with nearly transverse anterior edges (strongly oblique in *G. gracilis*); larger postorbital processes; a more longitudinally oval anterior fontanelle; parallel edges to the suborbital shelves; stronger anterior projections on the postorbital processes; possibly more posteriorly exserted hyomandibular facets; possibly lower occipital condyles.

***Galeus sauteri* and *G. schultzi*.** *Galeus sauteri* from Taiwan and possibly the Philippines, and *G. schultzi* from the Philippines are less similar to *G. gracilis* than other western North Pacific *Galeus*. They are characterised here from specimens and from the accounts of Nakaya (1967), Springer (1979), and Compagno (1984, 1988). *Galeus sauteri* and *G. schultzi* agree with *G. gracilis* in having a relatively long abdomen (PPS 11.5-14.5% TL versus 14.3-16.0% TL); low vertebral counts (see Table 2); relatively small size. *Galeus gracilis* may lie between *G. schultzi* (adults 254-297 mm TL) and *G. sauteri* (adults 354-450 mm TL). Both species differ from *G. gracilis* in their shorter prenarial snouts (PRN 0.6-0.8 of EYL versus 0.9-1.3); less pointed, more bluntly rounded snouts; stouter bodies; shorter, more compressed caudal peduncles (ACS/ANB ratio 0.2-0.3 versus 0.5-0.7); clasper tips reaching behind the anal-fin origin;

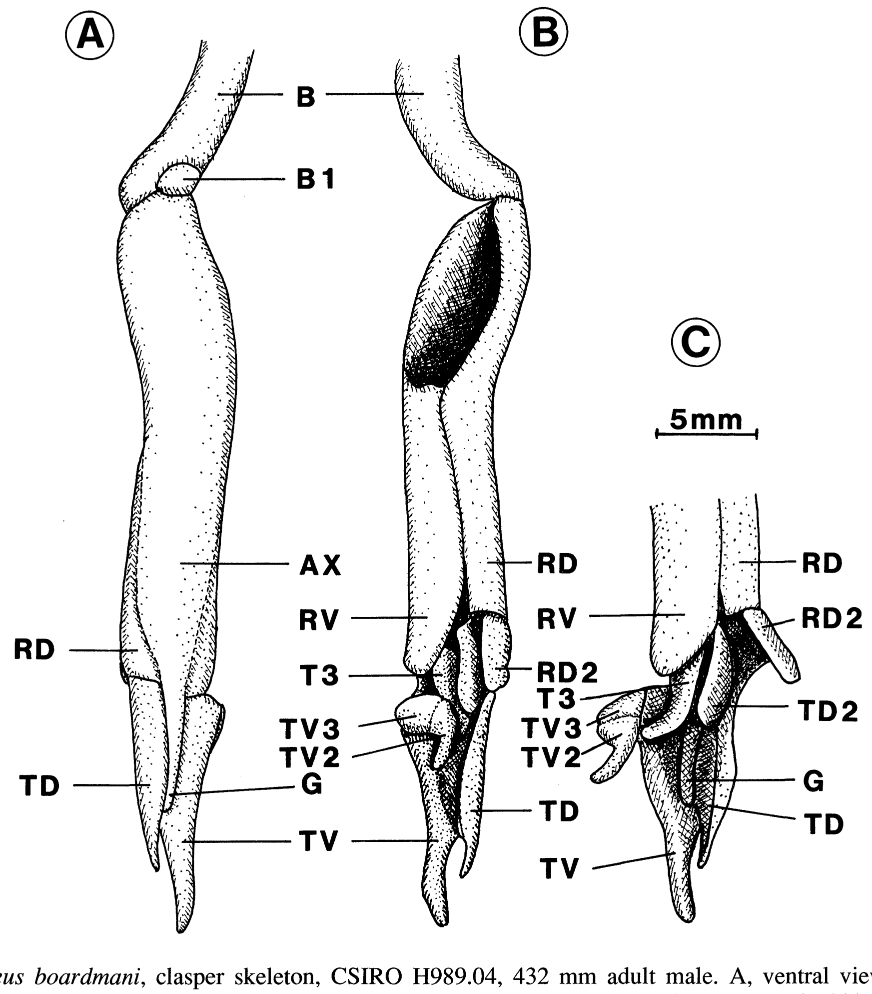

Fig.15. *Galeus boardmani*, clasper skeleton, CSIRO H989.04, 432 mm adult male. A, ventral view; B, dorsal view, terminal cartilages not dilated; C, dorsal view of glans, terminal cartilages spread. Abbreviations as in Figure 7. Illustration by L.J.V. Compagno.

somewhat larger pectoral fins (P1A 10.6-13.4% TL in *G. sauteri* and 12.3-12.6% TL in *G. schultzi* versus 9.7-11.0% TL); longer anal-fin base (12.6-16.9% TL in *G. sauteri* and over 13% TL in *G. schultzi*); poorly-developed saddles on the body and precaudal tail; dark markings on the hypural and terminal caudal-fin lobes (lacking in *G. gracilis*).

Galeus schultzi additionally differs from *G. gracilis* in its shorter preoral snout (5.4-5.9% TL versus 6.4-7.8% TL); smaller mouth (MOW 6.5-6.7% TL versus 7.0-8.1% TL); the long preanal ridge on the anal fin, bringing the anal-fin origin almost to the pelvic-fin insertions (absent in *G. gracilis*); shorter labial furrows (ULA about 0.7% TL versus 1.6-2.1% TL); possibly fewer tooth rows (48/less than 48 versus 54-57/54-62); possibly more elongated claspers, according to Springer (1979).

Galeus sauteri also differs from *G. gracilis* in having laterally situated eyes and reduced subocular ridges; more numerous tooth rows (70-78/82 versus 54-57/54-62); shorter claspers (CLO 7.3% TL versus 10.3-10.8% TL); hourglass-shaped claspers, with a broad base, narrow midshaft and expanded glans (Compagno, 1988, fig.13.20D; tapered in *G. gracilis*); broad, strongly twisted clasper tip; vestigial cover rhipidion (well developed in *G. gracilis*); prominent black blotches on the dorsal fins (dusky markings in *G. gracilis*); gray mouth (dark grey or black in *G. gracilis*); slightly more numerous intestinal valves (8-9, mean 8.7 in 6 *G. sauteri* versus 6-7).

The chondrocranium of *G. sauteri* (Fig.13I) differs from that of *G. gracilis* in having more widely spaced bases on the lateral rostral cartilages (distance between bases 1.5 times anterior fontanelle width in *G. sauteri*, about 0.9 in *G. gracilis*); smaller, more widely spaced nasal capsules; a broader anterior fontanelle and cranial roof; larger preorbital processes; larger otic capsules; possibly lower occipital condyles.

***Galeus arae* complex and *G. piperatus*.** The western North Atlantic *Galeus arae* and *G. piperatus* from the

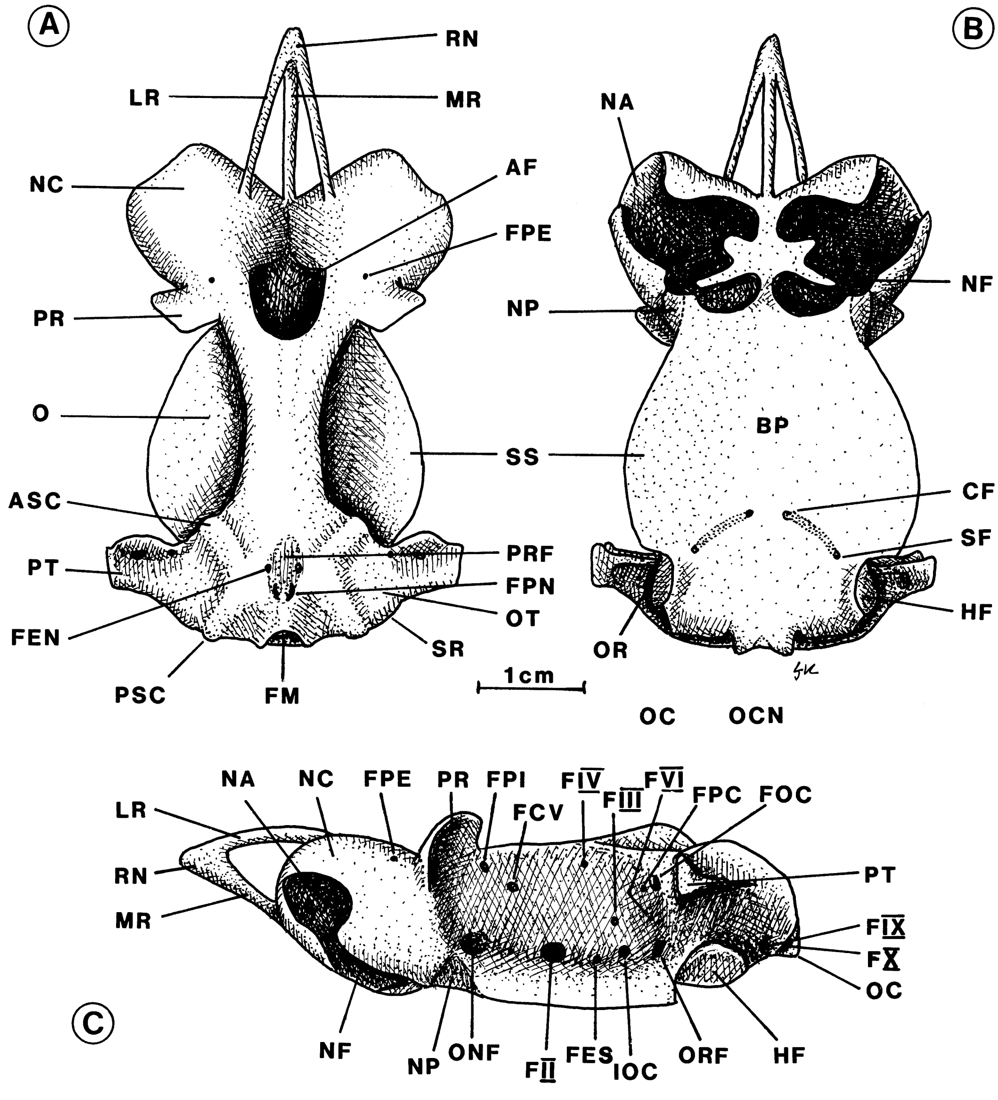

Fig.16. *Galeus boardmani*, chondrocranium from CSIRO H989.04, 432 mm adult male. A, dorsal view; B, ventral view; C, lateral view. Abbreviations as in Figure 9. Illustration by L.J.V. Compagno.

Gulf of California are very close, but certain aspects of the morphology of the latter are not well known. Additionally, *G. arae* was subdivided by Springer (1979) into three allopatric subspecies of uncertain status: the typical *G. arae arae* of the continental slopes from South Carolina south to Costa Rica; *G. a. antillensis* Springer, 1979, a Caribbean island form from the Straits of Florida to Cuba, Hispanola, Puerto Rico, and the Leeward Islands; *G. a. cadenati* Springer, 1966, from the continental slope off Panama and Colombia. Muñoz-Chapuli & Ortega (1985) suggested that Springer's arrangement was problematical because of differences in mode of reproduction between *G. a. antillensis* (possibly oviparous) and *G. a. arae* (ovoviviparous), and that this difference "would seem to be a specific character". *Galeus a. antillensis* and *G. a. cadenati* apparently attain a larger size than typical *G. a. arae*, and the little-known *G. a. cadenati* has a consistently longer anal-fin base and shorter anal-caudal and pelvic-anal spaces than the other two subspecies. For purposes of comparison with *G. gracilis*, the subspecies of *G. arae* are mostly considered together, although they may represent a complex with three separate species plus *G. piperatus* in a superspecies. Springer (1966) had originally described *G. a. cadenati* as a full species, but later (Springer, 1979) reduced its rank.

Data on *G. arae* are from specimens and Springer (1966, 1979), and on *G. piperatus* from Springer & Wagner (1967) and Hubbs & Taylor (1969). *Galeus arae* and *G. piperatus* agree with *G. gracilis* in being small (adults from 255-360 mm in *G. a. arae*, but up to 435 mm TL in *G. a. antillensis*, and 296-302 mm TL in *G. piperatus*) and in having similar tooth row and monospondylous vertebral counts. These species differ from *G. gracilis* in having a broadly rounded snout tip; larger eyes in adults (3.4-4.3% TL versus 3.2-3.3% TL); stouter bodies; shorter, broader precaudal tails with shorter pelvic-anal spaces (PAS/ANB 0.2-0.5 versus 0.8-1.0); shorter anal-caudal spaces (ACS/ANB 0.1-0.4 versus 0.5-0.7); shorter abdomens in adults (PPS 8.1-13.0% TL versus 14.3-16.0% TL); more cylindrical claspers with an hourglass or bilobate shape (Fig.12C); blunt clasper tips that extend behind the anal-fin origin; slightly larger pectoral fins in adults (P1A 10.5-12.2% TL in *G. arae* and 12.6-13.0% TL in *G. piperatus* versus 9.7-11.0% TL); slightly longer to considerably longer anal-fin bases (10.3-13.6% TL in *G. a. arae*, up to 15.0% TL in *G. a. cadenati* and 12.6-13.0 in *G. piperatus* versus 9.7-11.0% TL); a darker ground colour in adults, with either more numerous blotches and saddles or with no markings.

Galeus piperatus additionally differs from *G. gracilis* in having a slightly broader mouth (MOW 8.3-9.2% TL versus 7.0-8.1% TL) and fewer precaudal centra (66-72 versus 74-78), while *G. arae* differs from *G. gracilis* in having lateral eyes with the subocular ridge reduced (not known for *G. piperatus*). The claspers of *G. piperatus* are poorly known, but those of *G. arae* (Fig.12C) differ from *G. gracilis* in having a slightly longer glans (0.7 of distance from apopyle to clasper tip, versus 0.6); more twisted tips; prominent clasper hooks on the exorhipidion; a larger cover rhipidion; a larger exorhipidion.

The chondrocranium of *G. piperatus* is not known, but that of *G. arae* (*G. a. arae*, Fig.13A, not known in other subspecies) differs from *G. gracilis* in the more widely spaced bases of its lateral rostral cartilages (1.3 times the anterior fontanelle width versus 0.9 times); more laterally expanded nasal capsules (width across them 77% of NBL versus 71% of NBL); smaller, more laterally directed postorbital processes; more convex edges on the suborbital shelves; slightly larger otic capsules.

***Galeus atlanticus* and *G. melastomus*.** *Galeus melastomus* of the eastern North Atlantic has a smaller sympatric relative, *Galeus atlanticus*. These are compared in detail by Muñoz-Chapuli & Ortega (1985), and are characterised here from the account of these authors plus Leigh-Sharpe (1922) and Springer (1979) and from specimens of *G. melastomus*.

Neither of these species is particularly close to *G. gracilis* within *Galeus*, and both differ from it in being larger (adults 480-730+ mm in *G. melastomus* and 384-480 mm in *G. atlanticus*); having larger eyes when adult (over 4% TL versus 3.2-3.3% TL); stouter bodies; shorter precaudal tails with short pelvic-anal spaces (PAS/ANB 0.2-0.4 versus 0.8-1.0) and anal-caudal spaces (ACS/ANB about 0.2 versus 0.5-0.7); shorter abdomens (PAS 8.1-10.2% TL versus 14.3-16.0% TL); larger, broader pectoral fins (greater than 12.0% TL versus 9.7-11.0% TL); more numerous pectoral-fin radials (20-21 in *G. atlanticus* and 22-24 in *G. melastomus* versus 16) and narrower, more axially elongated pectoral-fin skeletons; longer anal-fin bases (greater than 14% TL versus 10.5-11.5% TL); interdorsal space less than the anal-fin base (greater in *G. gracilis*); and more numerous dark saddles and irregular spotting in adults.

Galeus melastomus additionally differs from *G. gracilis* in having lateral eyes with a weak subocular ridge (uncertain in *G. atlanticus*); more numerous tooth rows (69-78/79-84 versus 54-57/54-62); a more compressed caudal peduncle (CPH/CPW 1.9 versus 1.1-1.4); claspers more hourglass-shaped, with blunt, more twisted points; clasper glans shorter (0.4 of distance from apopyle to clasper tip versus 0.6); cover rhipidion vestigial; possibly no pseudosiphon; possibly a more angular exorhipidion; more numerous MP (37-39 versus 33-36) and total (141-151 versus 130) vertebral centra.

The chondrocrania of *G. atlanticus* (Fig.13B) and *G. melastomus* (Fig.13F) differ from that of *G. gracilis* in having more widely spaced bases on their lateral rostral cartilages (distance between bases 1.9 times the anterior fontanelle width in *G. atlanticus*, 1.5 in *G. melastomus* versus 0.9); larger preorbital processes; more posteriorly elongated anterior fontanelles; larger, higher, more laterally directed postorbital processes. That of *G. atlanticus* additionally differs from *G. gracilis* in having more laterally expanded nasal capsules; a narrower cranial roof; broader suborbital shelves; larger otic capsules.

***Galeus murinus* and *G. polli*.** *Galeus murinus* and *Galeus polli* are two eastern North Atlantic species that are not close to *G. gracilis* or to each other. Data on these species is from Cadenat (1959), Springer (1979), Compagno (1984, 1988), Muñoz-Chapuli & Ortega (1985) and specimens. Both agree with *G. gracilis* in their tapered claspers with pointed, moderately twisted clasper tips and in their MP vertebral counts. However, both have larger eyes (greater than 3.5% TL versus 3.2-3.3% TL); stouter bodies; shorter precaudal tails with short pelvic-anal spaces (PAS/ANB 0.2-0.3 versus 0.8-1.0) and anal-caudal spaces (ACS/ANB 0.1-0.2 versus 0.5-0.7); a vestigial cover rhipidion on their claspers; a more angular exorhipidion (more bulbous in *G. gracilis*); interdorsal space less than the anal-fin base (greater in *G. gracilis*); either a uniform dark colouration or a darker ground colour with more dark saddles and irregular spotting in adults.

Galeus murinus has a long abdomen and relatively small pectoral fins, as does *G. gracilis*, but additionally differs in its blunt snout with broadly rounded tip; shorter mouth; presence of a spur on the exorhipidion (Compagno, 1988, fig.13.20B); higher pelvic fins; higher anal fin (ANB/ANH 2.2 versus 3.0-3.7); a crest of enlarged denticles on the preventral caudal-fin margin; fewer PC centra (66-67 versus 74-78); greater size (adults 479-545 mm). *Galeus polli* attains a similar size (adults 255-385 mm TL) to *G. gracilis*, but additionally differs in having lateral eyes, with the subocular ridge reduced; possibly more tooth rows (69/65 versus 54-57/54-62); more compressed caudal peduncle (CPH/CPW 1.6-1.7 versus 1.1-1.4); shorter abdomen (7.8-13.5% TL versus 14.3-16.0% TL); shorter claspers (CLO 5.0-6.3% TL versus 10.3-10.8% TL); clasper hooks on the exorhipidion; more numerous pectoral-fin radials (19 versus 16); a larger anal-fin base (greater than 14% TL versus 10.5-11.5% TL); and more numerous intestinal valve turns (12-14, mean 13.5, sd 0.5, in 16 specimens counted versus 6-7).

The chondrocranium of *G. murinus* has not been studied, but that of *G. polli* (Fig.13H) differs from *G. gracilis* in the more widely spaced bases of its lateral rostral cartilages (1.3 times the anterior fontanelle width versus 0.9 times); smaller, more laterally separated nasal capsules; larger, more posteriorly expanded anterior fontanelle; broader cranial roof; narrower, higher, more laterally directed postorbital processes.

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APPENDIX

Table 1. *Galeus gracilis* n.sp. Proportional dimensions of type specimens as percentages of total length (TL in mm).

Coll. No.	CSIRO H1208-01 Adult female Holotype	CSIRO CA3304 Adult female Paratypes	CSIRO CA4477 Adult male	CSIRO CA4478 Adult male
TL	335	312	329	333
PCL	74.6	71.2	79.0	72.7
PRN	4.2	3.8	4.0	3.0
POR	7.8	6.4	7.3	6.6
POB	7.8	6.7	7.6	6.6
PSP	11.6	10.6	12.2	11.1
PGI	16.1	13.8	16.7	15.3
HDL	22.1	18.3	21.6	19.8
PP1	21.5	19.2	21.3	19.5
PP2	42.1	37.2	40.1	38.4
SVL	44.5	40.7	43.5	42.0
PAL	57.9	54.2	58.4	54.7
PD1	46.6	43.6	44.4	43.2
PD2	65.1	62.8	64.7	60.4
IDS	12.8	12.2	13.4	12.6
DCS	4.2	2.9	3.6	3.6
PPS	15.5	16.0	14.3	15.6
PAS	10.1	8.3	10.3	9.3
ACS	6.3	6.4	7.6	6.0
EYL	3.3	3.2	3.3	3.3
EYH	1.8	1.0	1.2	0.9
INO	6.6	6.4	6.4	6.6
NOW	2.4	2.2	2.4	2.4
INW	3.0	2.6	2.4	2.4
ANF	1.2	0.6	0.6	1.2
SPL	0.9	0.6	0.6	1.2
ESL	0.6	1.0	1.4	0.9
MOL	3.3	3.2	3.8	3.0
MOW	8.1	7.1	7.0	7.8
ULA	1.8	1.6	2.1	1.8
LLA	2.4	1.9	2.1	2.4
GS1	1.8	1.6	1.2	1.5
GS2	1.8	1.6	1.2	1.8
GS3	1.8	1.6	0.9	2.1
GS4	1.8	1.3	1.2	1.8
GS5	2.1	0.6	0.9	1.2
HDH	8.7	6.7	7.0	6.3
HDW	11.6	9.6	9.4	10.5
TRH	11.0	7.1	6.7	8.1
TRW	9.6	8.0	8.2	8.7
CPH	3.0	3.2	3.0	3.0
CPW	2.7	2.2	2.7	2.4
GIR	30.4	21.5	25.8	22.5
P1L	11.3	10.9	10.3	10.8
P1A	11.0	10.9	9.7	10.2
P1B	6.0	6.4	5.2	5.7
P1H	7.5	8.0	8.8	8.1
P1I	6.9	4.8	4.6	5.4
P1P	8.7	7.1	7.0	7.8
P2L	11.3	10.3	11.2	10.8
P2A	5.4	4.8	6.4	6.0
P2B	7.5	7.1	7.3	7.8
P2H	3.0	3.8	3.6	3.0
P2I	4.5	2.9	3.3	3.0
P2P	7.5	6.7	4.9	4.8

Table 1 (cont'd).

Coll. No.	CSIRO H1208-01 Adult female Holotype	CSIRO CA3304 Adult female Paratypes	CSIRO CA4477 Adult male	CSIRO CA4478 Adult male
CLO	–	–	7.3	7.2
CLI	–	–	10.3	10.8
CLB	–	–	1.5	1.5
D1L	8.7	8.7	10.0	9.3
D1A	8.4	8.7	10.0	9.3
D1B	5.7	6.1	7.9	7.2
D1H	4.8	3.8	4.0	4.2
D1I	2.1	2.6	2.7	2.4
D1P	3.9	3.2	2.6	3.3
D2L	8.1	7.7	8.2	8.1
D2A	7.8	7.4	7.9	7.5
D2B	5.7	5.4	5.5	6.0
D2H	3.3	3.5	3.3	3.9
D2I	2.4	2.2	2.4	2.4
D2P	3.3	2.9	2.7	2.7
ANL	12.5	12.5	13.4	13.8
ANA	7.5	7.4	7.0	9.0
ANB	11.0	10.6	11.6	11.1
ANH	3.0	3.5	3.3	3.3
ANI	1.5	1.9	1.8	1.8
ANP	7.2	6.4	7.3	6.6
CDM	25.4	27.6	26.4	27.9
CPV	9.0	8.3	8.2	10.2
CPL+	11.6	15.1	13.4	13.5
CST	3.9	4.2	3.6	4.8
CTR	4.2	4.2	4.0	3.9
CTL	5.4	5.8	5.5	6.0
DAO	6.9	7.1	7.6	7.2
DAI	1.5	1.3	1.8	2.7

Table 2. Vertebral counts, ratios and statistics for *Galeus* specimens examined here. Abbreviations for type specimens: HT – holotype; PT – paratype; SN – syntype.

G. gracilis		T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
CSIRO H1208-01 HT		335	36	42	56	78	134	26.8	31.3	41.7	1.2	1.6	141	86
CSIRO CA3304 PT		317	34	41	55	75	130	26.1	31.5	42.3	1.2	1.6	146	133
CSIRO CA4477 PT		329	35	43	–	78	–	–	–	–	1.2	–	133	117
CSIRO CA4478 PT		333	33	41	–	74	–	–	–	–	1.2	–	133	100
	range		33	41	55	74	130	26.1	31.3	41.7	1.2	1.6	133	86
			36	43	56	78	134	26.8	31.5	42.3	1.2	1.6	146	133
	mean		34.5	41.8	55.5	76.3	132.0	26.5	31.4	42.0	1.2	1.6	138.3	108.9
	SD		1.1	0.8	0.5	1.8	2.0	0.4	0.1	0.3	0.0	0.0	5.2	17.8
	CV		3.2	2.0	0.9	2.3	1.5	1.3	0.3	0.6	2.4	2.0	3.8	16.4
	N		4	4	2	4	2	2	2	2	4	2	4	4

G. arae		T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU 66816		289	34	40	59	74	131	25.9	30.5	43.5	1.2	1.7	169	135
SU 66816		272	35	41	57	76	136	25.7	30.1	44.1	1.2	1.7	167	125
ORE 3627		255	36	42	60	78	136	26.4	30.8	42.6	1.2	1.6	162	124
ORE 3627		277	35	41	58	76	136	25.7	30.1	44.1	1.2	1.7	163	130
ORE 3627		270	35	40	60	75	129	27.1	31.0	41.8	1.1	1.5	147	116
ORE 3627		278	36	38	54	74	133	27.0	28.5	44.3	1.1	1.6	141	126
SU 66814		205	35	42	59	77	133	26.3	31.5	42.1	1.2	1.6	164	129
SU 66814		270	35	42	56	77	134	26.1	31.3	42.5	1.2	1.6	153	121
SU 66814		215	34	43	57	77	138	24.6	31.1	44.2	1.3	1.8	170	121
SU 66814		275	35	42	61	77	134	26.1	31.3	42.5	1.2	1.6	156	119
SU 66814		250	36	41	57	77	133	27.0	30.8	42.1	1.1	1.6	140	124
SU 66814		206	35	40	56	75	135	25.9	29.6	44.4	1.1	1.7	164	139
SU 66814		260	35	43	60	78	136	25.7	31.6	42.6	1.2	1.7	147	138
SU 66814		232	35	42	58	77	133	26.3	31.5	42.1	1.2	1.6	146	112
SU 66814		206	35	42	56	77	133	26.3	31.5	42.1	1.2	1.6	167	125
SU 66814		273	36	37	56	73	129	27.9	28.6	43.4	1.0	1.6	139	83
SU 66814		198	35	40	56	75	131	26.3	30.1	43.4	1.1	1.6	160	133
	range		34	37	54	73	129	24.6	28.5	41.8	1.0	1.5	139	83
			36	43	61	78	138	27.9	31.6	44.4	1.3	1.8	170	139
	mean		35.1	40.9	57.6	76.1	133.6	26.3	30.6	43.1	1.2	1.6	156.0	123.5
	SD		0.6	1.6	1.9	1.4	2.4	0.7	0.9	0.9	0.1	0.1	10.4	12.3
	CV		1.7	3.9	3.3	1.9	1.8	2.7	3.1	2.1	4.8	4.0	6.7	10.0
	N		17	17	17	17	17	17	17	17	17	17	17	17

G. boardmani	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
AMS IA2483 HT	542	37	58	53	95	148	25	39.1	35.8	1.6	1.4	196	121

G. eastmani	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU 35469	342	36	49	65	85	150	24	32.6	43.3	1.4	1.8	140	112
SU 7740 HT	336	33	50	58	83	141	23.4	35.4	41.1	1.5	1.8	159	117

G. melastomus	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU 20604	380	37	46	60	83	143	25.8	32.1	41.9	1.2	1.6	168	119

Table 2 (cont'd).

G. sauteri	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU 21261 ST	370	33	41	54	74	128	25.7	32.0	42.1	1.2	1.6	157	127
SU 21261 ST	362	32	43	53	75	128	25.0	33.5	41.4	1.3	1.7	148	126
SU 21261 ST	369	33	41	51	74	125	26.4	32.8	40.8	1.2	1.5	123	123
SU 21261 ST	366	33	43	49	76	125	26.4	34.4	39.2	1.3	1.5	138	118
CAS 1971-VI:11	382	33	40	49	73	122	27.0	32.7	40.1	1.2	1.5	173	131
CAS 1971-VI:11	383	33	40	50	73	123	26.8	32.5	40.6	1.2	1.5	140	117
CAS 1972-III:14	450	34	39	49	73	122	27.8	31.9	40.1	1.1	1.4	154	123
CAS 34152	303	38	38	56	76	132	28.7	28.7	42.4	1.0	1.5	142	129
CAS 34152	301	32	41	52	73	125	25.6	32.8	41.6	1.3	1.6	144	108
	range	32	38	49	73	122	25.0	28.7	39.2	1.0	1.4	123	108
		38	43	56	76	132	28.7	34.4	41.0	1.3	1.7	173	131
	mean	33.4	40.7	51.4	74.1	125.6	26.6	32.4	41.0	1.2	1.5	146.5	122.4
	SD	1.7	1.6	2.4	1.2	3.1	1.1	1.5	1.0	0.1	0.1	13.1	6.6
	CV	5.1	3.8	4.6	1.6	2.5	4.1	4.5	2.4	7.8	4.9	9.0	5.4
	N	9	9	9	9	9	9	9	9	9	9	9	9

G. schultzi	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
CAS 34852	155	32	41	48	73	121	26.4	33.8	39.6	1.3	1.5	133	120
CAS 34852	143	32	41	51	73	124	25.8	33.0	41.1	1.3	1.6	157	100
CAS 33843	177	33	44	53	77	130	25.3	33.8	40.7	1.3	1.6	167	136
CAS 34556	165	33	47	48	80	128	25.7	36.7	37.5	1.4	1.5	175	127
CAS 34556	182	35	44	57	79	136	25.7	32.3	41.9	1.3	1.6	142	131
	range	32	41	48	73	121	25.3	32.3	37.5	1.3	1.5	133	100
		35	47	57	80	136	26.4	36.7	40.2	1.4	1.6	175	136
	mean	33.0	43.4	51.4	76.4	127.8	25.8	34.0	40.2	1.3	1.6	154.8	122.9
	SD	1.1	2.2	3.4	2.9	5.2	0.3	1.5	1.5	0.1	0.1	15.4	12.6
	CV	3.3	5.2	6.6	3.8	4.0	1.3	4.4	3.8	4.5	4.3	10.0	10.3
	N	5	5	5	5	5	5	5	5	5	5	5	5